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THE STRUCTURE AND DEVELOPMENT OF OPHIOGLOSSUM PALMATUM

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(WITH TWENTY-ONE FIGURES)

Ever since its discovery in Hispaniola by Plumier early in the eighteenth century *Ophioglossum palmatum* L. has attracted attention, partly because of its unusual form and partly no doubt because of its rarity. In the original description of the plant Plumier (1705) says: "Je n'ay jamais rencontré cette plante qu'une seule fois, dans tous mes trois voyages dans les Isles de l'Amérique." Considering the general rarity of the plant, it comes as a matter of surprise to read in a letter from the late Dr. J. K. Small: "Forty or fifty years years ago one could go to the edge of the Everglades back of Miami (Florida) and collect it by the wagon load. Today not a leaf can be found there."

MATERIAL AND METHODS

Through Doctor Small's kindness material was preserved in the field during one of his last visits to Florida, namely in November 1936. In order to secure a series of stages in development, I visited one of the Florida stations in January 1938, on which occasion I was favored by the cooperation of Dr. H. H. Hume and Mr. Erdman West, both of the Florida Agricultural Experiment Station, also of Dr. E. P. St. John and Dr. R. P. St. John. Hearty thanks are here extended to these botanists, especially for providing the ladders which were necessary to enable one to dislodge the plants from their position in the decaying matter beneath the crowns of the palmettoes, *Sabal Palmetto* (Walt.) Todd, in company with *Polypodium aureum* L. and *Vittaria lineata* (L.) Sw. A second visit to the same station was made in April 1939, on which occasion I had the help of Professor M. A. Johnson of Rutgers University as well as of the St. John brothers. On these occasions an effort was made to secure gametophytes, but unfortunately without success. Even the young sporophytes appear to have arisen as buds from roots of older plants (v. Bower 1911).

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Most of the material was fixed in formalin-acetic-alcohol, but for the young spikes Allen's modification ("PFA[3]") of Bouin was used. For staining developing sporangia iron alum haematoxylin followed by gold orange proved to be entirely satisfactory, although in some cases the safranin-fast green combination was used. Picro-aniline blue seemed to be on the whole the most suitable stain for the mycorrhizae. Methods for clearing leaves proved to be of small value in tracing the course of the vascular bundles—even series of sections cut freehand and mounted in glycerine gave superior results.

In addition to the microscopic study a survey of the superficial features has been made of the numerous specimens represented in the herbaria at Kew, the British Museum, and the New York Botanical Garden. An examination of all available illustrations of the plant leads to the conclusion that many of them are distinctly unsatisfactory in their attempt to display the critical features.

The objects of the present study have been to find to what extent development in this species (genus?) differs from that of members of the group *Euophioglossum;* to examine in a sufficient number of individuals the attachment of the fertile spikes; and to attempt a revaluation of the different theories which have been proposed as to the morphological nature of the spike.

The earliest work on the internal structure of this plant appears to have been by Bertrand and Cornaille (1902), who figure a section through a leaf-stalk. In 1904 Bower was able from a Jamaica specimen to trace the origin of the vascular strands which supply the spikes. These results were confirmed and an analysis of the stem structure was made in 1911, when he had access to another plant from the same source. This work was supplemented by careful study of many herbarium sheets. At about the same time Campbell (1911) in his work on the Eusporangiatae made brief reference to certain features of root and leaf. Apparently no material was available to the previous workers for study of the development of sporangia and spores.

THE ROOT

The roots—all adventitious in the mature plant—are numerous and may reach a length of 240 mm., with diameter from 1.5 to 2 mm., penetrating the loose litter between the dead leaf bases of the palmetto, as we find the plant growing in Florida. Occasional branchings which are to be regarded as dichotomies occur. The absence of root-hairs is in keeping with the mycorrhizal habit. At a short distance back of the region covered by the root-cap it is seen that the outer layer of the root, which would ordinarily be developed as a piliferous layer, comes to have a firm wall which is impregnated with a highly impervious substance which stains with safranin, but does not

yield reactions for lignin or suberin. The outer wall of the cells in question is especially thickened in older regions of a root, and may assume a yellow color. With this may be compared the observations of Petry (1914) on the root of *O. pendulum*. The general features of the mature root are represented in figures 5, 17, in which it may be made out that the external layer of cells is followed by an outer cortex devoid of intercellular spaces and having a thickness of from five to seven cells. These cells have a transverse diameter of about 70 μ and a length of about 300 μ; they contain numerous very small starch grains, and the inner part of the layer (2–3 cells thick) may contain a fungus. The inner cortex has a thickness of 4–5 cell diameters and its cells display a thickening which approaches collenchyma; where three cells meet the walls are markedly thickened and the secondary wall stains like cellulose, while the primary wall is well developed in the "corner" regions, taking a strong safranin stain. But in the innermost parts of the cortex the primary wall disappears, leaving the usual triangular intercellular spaces. The endodermis displays a plain Caspary's band. The stele has an average diameter of about 0.4 mm., and shows a continuous mass of xylem which is diarch in a large majority of the roots which have been examined, although, as noted by Campbell (1911), the triarch condition also occurs, and both the diarch and triarch condition is to be seen in different roots of the same plant. Moreover a triarch root may distally become diarch, especially after a dichotomy. A section through the stele of one of the triarch roots is shown in figure 5. With this may be contrasted the stele of *O. fibrosum*, figured by Maheshwari and Singh (1934), in which species the three xylem groups are widely separated.

Mycorrhiza. The occurrence of a fungus in the outer cortical layer has already been mentioned, and is conspicuous when present. Bower (1911) refers to "the presence of endotrophic mycorrhiza, though not in such profuse development as the habit of the plant might lead one to expect." Many root sections fail to show fungi, even at a distance of some centimeters from the tip. Moreover the mycorrhizal zone may extend only part way around the root, indicating a local infection. In the Florida material very few cells containing filamentous hyphae ("fungus host cells") have been found, but most have passed into the digestive stage, i.e., they show irregular lumps of varying size and shape occupying a large part of the cell, not however including the nucleus. Coenocytic hyphae but no reproductive cells have been observed, so it would not be possible to identify the fungus as *Stigeosporium Marattiacearum*. In this action we thus follow Burgeff (1938) in his discussion of the mycorrhizae of *O. pendulum*.

The tip region of the root cut in longitudinal and transverse planes shows a tetrahedral apical cell with four cutting faces, and is thus typical of the order (Bower 1926). Mitoses in adjoining cells are frequent, indicating that

growth was rapid in the early spring period in which the material was collected. The mitotic figures contain a very large number of small narrow chromosomes, and could not be counted in this part of the plant (*vide infra*). No irregular segmentation similar to that observed in *O. pendulum* by Petry (1914), and by him attributed to slow growth, were found in the Florida material. Differentiation of the xylem within 4 mm. of the tip was found in two of the roots. This xylem already displayed the type of tertiary thickening which is characteristic of the tracheids in Ophioglossales.

THE STEM

The rhizome has a definitely stocky form in the Florida specimens, mature individuals having an average diameter of 9 mm. and a length approximately the same. Bower gives the diameter of his Jamaica specimen as ¾ inch, which appears to be rather above the average. Moreover the Florida plants usually show from three to four functional leaves at one time instead of the single one which is represented in some herbarium specimens.

Judging from the number of withered leaf bases surrounding the larger rhizomes, and from the prevalence of smaller plants, growth of the stem is slow. This results in a crowding of the leaves, involving complexity of the vascular skeleton. Bower succeeded in resolving the network into a fairly narrow dictyostele in which the vascular supply of a leaf arises as two strands, one from each side of a wide gap. A quite peculiar condition exists in the form of a "commissure" stretching between the two strands immediately above the point of exit from the stele. I have been able to confirm the foregoing as a general statement; but examination of a larger number of rhizomes indicates that the plan is subject to variation. For example, the commissure may fail to appear in some of the gaps; a root may or may not arise from the commissure; roots in some cases strike downward through the pith instead of the cortex; the double leaf trace may extend through the cortex and petiole without branching for a much greater distance than is shown in Bower's figure 4 (1911); a diarch root may lie beside a triarch one. These variations well match the wide differences in number of lobes and of fertile spikes which different individuals show.

The bundles which constitute the stele are ectophloic, with protoxylem ill-defined but mostly endarch. Secondary growth is lacking. The tracheids have the exceptional combination of spirals and pits which is characteristic of Ophioglossales (Loughridge 1932). In the position of an external endodermis some individuals have a layer whose cells are filled with dark-staining fine granules, while other individuals have some cells of the layer thick-walled, reticulate, and taking a definite stain with safranin. But in other stems no endodermis can be distinguished, and in none has a typical Caspary's band been seen. Perhaps the specialized layer should be regarded as

pericycle. No fungal hyphae have been observed in any of the rhizomes, but in some cases starch grains are abundant, although they may be entirely absent from a rhizome.

THE LEAF

The branching of the sterile segment of the leaf has won for the plant the common name "hand fern" (Plumier, l.c., says "à peu prés comme une main ouverte," as well as the specific designation *palmatum*. These words, however, appear to misrepresent the true nature of the lobing. Bitter (1900) refers to "2–3 fachen Dichotomien," and this feature was first brought to my attention by inspection of several specimens in the Herbarium of the

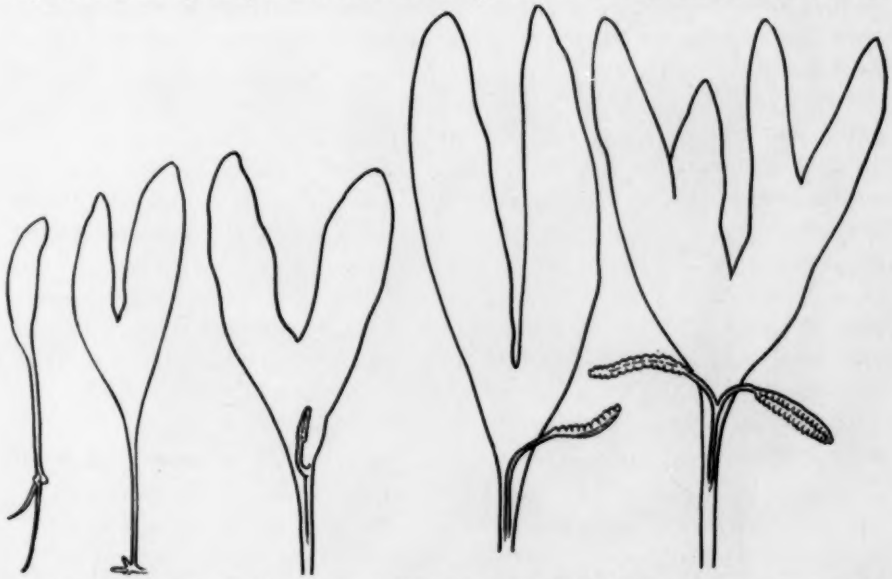

FIG. 1. Leaves showing stages in dichotomy. The two youngest leaves are sterile; the third leaf shows the unusual condition of a single marginal spike.

New York Botanical Garden. These plants were collected in Sta. Catharina, Brazil, and very clearly show the sterile part of the leaf twice dichotomous, with ribbon-shaped lobes. I have not been able to inspect Plumier's type specimen, but his illustration (l.c., pl. 163) shows two plants each with four nearly equal lobes, so we may infer that his specimens did not suggest dichotomy. Hooker, who had access to specimens from Mauritius, seems to have had shadowy ideas on the critical features, for his plate IV (1836) does not bring out the dichotomy and fails to indicate clearly the region of insertion of the five fertile spikes. The figure of Martius (1859, pl. 9) is much more satisfactory, showing ten fertile spikes, all marginal except the lowest, and the sterile segment twice dichotomous. Plate 7 of Bower's *Studies* (1896)

shows two plants with dichotomous branching, but the author appears at the time of writing not to have been impressed by the fundamental nature of dichotomy in pteridophytes, for he merely mentions (p. 29) with regard to the specimen "in fig. 118, four lobes of the sterile (two incompletely separate), and two fertile spikes." Clausen (1938) uses the expression "palmately lobed or divided," which of course expresses the form of many leaves, but gives no hint as to the real nature of the lobing. It will readily be seen that unequal development of the lobes or sinuses of a twice dichotomous blade would produce the more or less palmate effect presented by the majority of specimens. That the plan of the leaf in *O. palmatum* is inherently dichotomous is rendered probable also by the venation, which is plainly reticulate (fig. 2), but has not departed as widely from the dichotomous type as is the case in some other species, e.g., *O. Engelmanni* Prantl. It may be observed from figure 2 that in *O. palmatum* the meshes are relatively elongated, and the secondary network within the primary meshes poorly developed. Observation of young plants (fig. 1) shows the first leaf undivided and sterile, later leaves 2-lobed and either sterile or fertile, while still later leaves are more or less clearly twice dichotomous and fertile, with an increasing number of lobes and of spikes.

As seen in transverse section, the blade of the sterile segment has a thickness of about 0.5 mm., with no differentiation of a palisade. A cuticle is moderately developed, and small stomata are frequent on the lower surface. The vascular bundles are small and of the ordinary collateral type.

In the leaf-stalk, the epidermis, while only moderately thick-walled, is quite resistant to diffusion of aqueous fluids. The ground tissue is thin-

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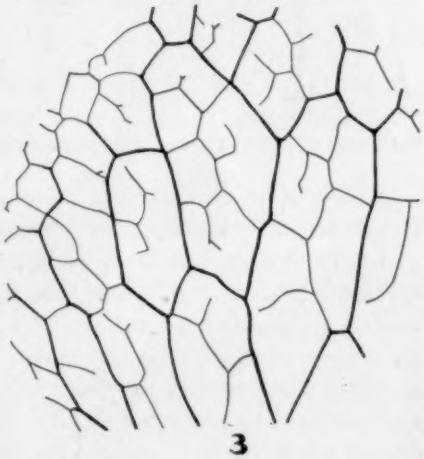

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FIG. 2. Plan of venation in leaf of *O. palmatum*. FIG. 3. Plan of venation in *O. Engelmanni*. In this species the secondary reticulum is well developed. Both × 5.

walled and undifferentiated, with cells devoid of starch. The number of vascular strands ranges from two at the base to twelve or more further up. The course of these has been clearly traced by Bower (1911, figs. 17–20) who makes the point that the strands not only increase in number upward, but anastomose and form a broad C-shaped group with the opening directed adaxially. In the upper part of the petiole the group closes so as to form a practically complete circular ring of bundles, although this is somewhat flattened adaxially in agreement with the shape of the petiole. I have been able to fully verify these observations by means of series through a number of petioles. The bundles are collateral and for the most part have endarch xylem. Larger bundles with distinctly mesarch structure are also found (fig. 6), having the protoxylem nearer the adaxial side. The tracheids of the

FIG. 4. Fertile spikes, all but the left-hand one abnormal.

metaxylem have the same type of thickening as is found in the stem. Shortly before petiole merges into blade, several bundles branch off from the adaxial side of the ring and curve adaxially to supply the lowest fertile spike. In agreement with Bower I fail to identify these bundles with the ones which close up the "C" into an "O," because several anastomoses have occurred at this position; all that can be said is that the strands in question arise from the region of junction of the edges of the C, and that after their departure the C-form is resumed.

An example of the rare cases in which there are two basal spikes in place of one (see pl. 22 in Bower 1911) has also been examined in a series of sections. The only difference from the normal is that from the adaxial group

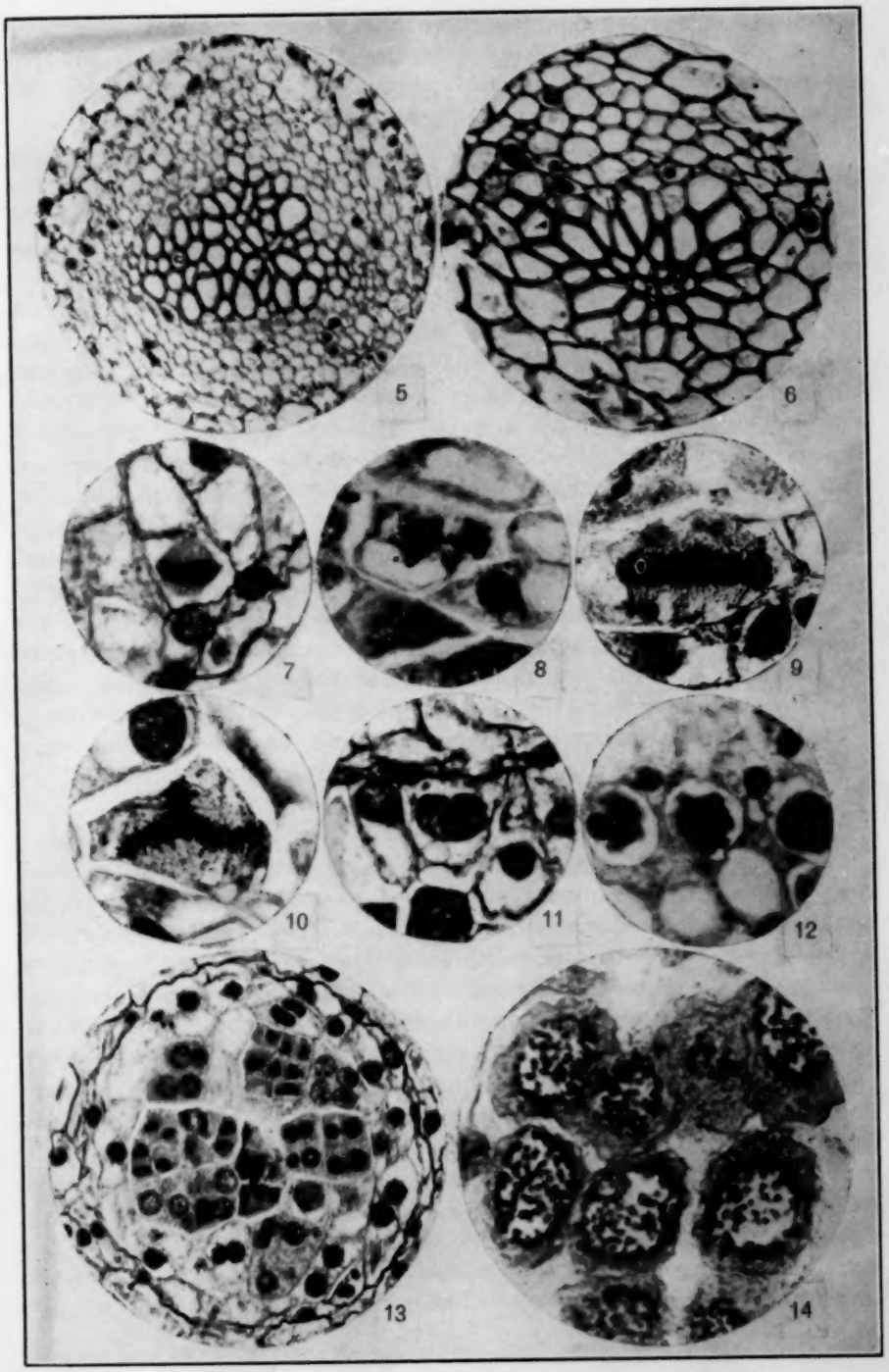
of petiolar bundles seven, lying side by side, separate slightly into a set of four and one of three bundles, each of the sets supplying one of the contiguous spikes, and leaving the petiole with a C-shaped vascular supply. Very rarely cases occur where the stalk in median position forks and gives rise to two spikes. In all the plants which have come under my observation, the vascular supply of the higher spikes arises as one or more bundles from the margin of the C, exactly as figured by Bower (1911, figs. 17–20).

Since in his paper of 1911 Bower has gone to some pains to establish the thesis that, with the exception of the lowest spike, "the insertion of the rest is usually intra-marginal" (p. 295), I have examined a considerable quantity of the Florida material to test the validity of this view. The plants in question had been preserved in liquid, and were cut free-hand into a series of sections which were mounted in glycerin. From a study of this material I can say that the uniform position of the upper spikes is marginal. It is necessary here to define what to my mind constitutes "marginal," and I have no hesitation in deciding this on the basis of vascular connection. To be explicit, I regard a spike as marginal when its vascular supply arises from the margin of the vascular system of the leaf. Bower's figures 17–20 in the paper of 1911 admirably illustrate the definition. If the vascular anatomy cannot be relied on to settle so simple a point as this, I fail to see much occasion for introducing anatomical evidence. For this reason I cannot see the significance (I do not question the accuracy) of Bower's figures 7–10, which are used to validate the statement (1911, p. 283) "whatever the vascular connections may be, the spikes of *O. palmatum* are in their prime origin intra-marginal."

As far as the mature spikes are concerned, there is a decided advantage in having access to material preserved in liquid, for the spikes are frequently decurrent to a marked degree, the stalk of a spike forming a distinct ridge upon the surface of the leaf. In a herbarium specimen this feature is apt not to be apparent, and the vascular system of a spike may be inserted on that of the leaf at a point some millimeters below the level where the stalk joins the surface of the petiole. In other words, the lower part of the stalk of a spike is in such cases fused with the petiole just as the basal part of the filament of a stamen may be fused with the surface of a corolla. In both cases

Explanation of figures 5–14

FIG. 5. Stele of triarch root. × 100. FIG. 6. Mesarch bundle from petiole. × 240. FIG. 7. Nucleus of tapetal cell in metaphase. × 250. FIG. 8. Two dividing nuclei in cell of tapetum. × 250. FIG. 9. Heteroploid nucleus of tapetal cell in metaphase. × 400. FIG. 10. Abnormal mitosis of tapetal cell. × 600. FIG. 11. Incompletely divided nucleus in tapetal cell. × 400. FIG. 12. Tapetal plasmodium with nuclei, also dividing sporocytes. × 275. FIG. 13. General view of sporangium showing the apparent wall, tapetum with several binucleate cells, sporogenous cells in various stages in different "blocks." × 95. FIG. 14. Diakinesis in sporocytes. × 525.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such fusion is to be regarded as a subsequent occurrence. The Florida material shows numerous cases where one or more of the upper spikes are inserted at a point at last 3 mm. inward from the edge of the leaf in the region where leaf-stalk widens into blade; when the vascular bundles of such spikes are traced downward they invariably join an edge of the C-shaped system of the petiole, which at this level has flattened out more or less. In view of the uniformity displayed by this preserved material, it is suggested that the specimens shown in Bower's figures 120 and 121 (1896), having an unusually large number of spikes irregularly placed, may represent abnormalities.

STRUCTURE OF THE FERTILE SPIKE

The general features of these rather large organs (30–40 mm. long and 5 mm. wide) are well known. There appears to be no constant difference between the spikes which are attached in the median adaxial region and those which arise toward the margin. The number of bundles at a level not more than 2 mm. above the point of attachment of the spike varies from one to three in the lateral spikes, and from two to four or occasionally five in median spikes. As the spore-bearing part of the spike is reached, a central bundle is found, with a slender bundle on each side, toward the sporangia. Numerous anastomoses occur between the bundles, and small branches are given off right and left into the spaces between the sporangia. When mature these organs have a diameter of ca. 1 mm., and are deeply infolded on the side toward the axis of the spike, so that their shape is distinctly reniform.

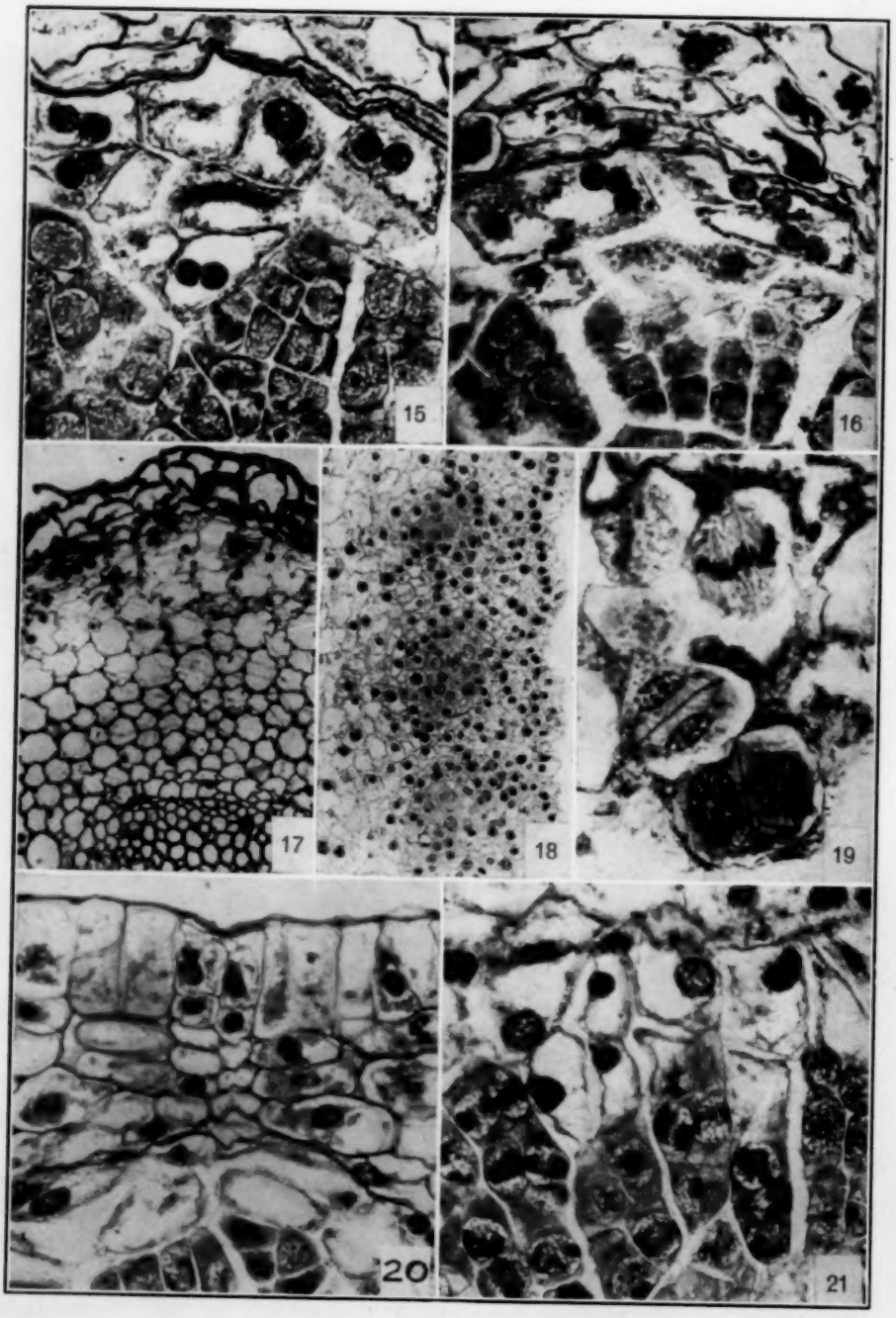
The most extensive contributions on spore development in the group have been made by Beer (1906), Cardiff (1905), and Stevens (1905).

DEVELOPMENT OF THE SPORANGIUM

The youngest fertile spikes represented in my material have a length of 2–3 mm. and a diameter up to 0.4 mm. The scanty material indicates that the apical cell is a pyramid with four cutting faces. A short distance below the apex is a somewhat indefinite indication of four unequal quadrants in one or more of which a cell is seen to have cut off segments. These observations correspond with Bower's findings in *O. reticulatum* (1896). Apparently my material is too young to show the origin of the sporangiogenic bands, for none of the cells differ from the rest in density of the protoplasm. The next stage represented in the Florida material (fig. 18) shows the sporogenous tissue segregated into two rows of well-defined nearly spherical groups having a diameter of about 0.2 mm., and sunken below the surface of the spike by about four layers of wall cells. In these groups the cells are much less vacuolate than are the wall cells, and hence stand out clearly. At this stage none of the cells can be identified as tapetal. Frequent mitoses are found in the sporogenous groups, which grow until they reach a diameter

of at least 0.25 mm. without further differentiation. During this stage at least four successive divisions of the sporogenous cells probably occur, resulting in the formation of groups of sporocytes. During the growth period the cells vary in shape but are mostly rectangular rather than polygonal, are fitted tightly together, and are separated by thin but clear walls. The nuclei measure about 20 μ in diameter, except in scattered cells in which divisions fail to occur and the nuclei may be over 30 μ wide. As the divisions proceed, the walls begin to separate, a process which cannot be attributed altogether to shrinkage during preparation of the material, because at this stage there is a marked increase in the dimensions of a sporangium, leading to production of a cavity which becomes occupied by tapetal plasmodium as well as developing spores. The dividing sporogenous cells adhere to each other in the so-called blocks, which are said to be characteristic rather of *Botrychium*, but are sometimes rather pronounced in *O. palmatum* (fig. 13). It is noticeable that cell-division is not simultaneous in different blocks, hence the spotty appearance of a developing sporangium. In some of the blocks eight regularly arrranged sporocytes may be seen, with indications of a second layer beneath the group of eight seen in the plane of the section. Before the blocks entirely break up some of the sporocytes have passed into the leptonema stage of meiosis, so that their nuclei present an entirely different appearance from that of the adjoining tapetal nuclei or of the other stages in development of sporogenous cells. Certain nuclei show a stage much resembling a "leptotène bouquet"; it is regarded as possible that these may be the result of imperfect fixation. As the sporocytes become separated and float in the plasmodium, pairing of chromosomes can be made out, and older cells have their nuclei plainly in diakinesis (fig. 14); here the chromosomes, usually slender as well as small, have become exceedingly short and stubby, and can be interpreted as tetrads. In other sporocytes (fig. 19) the chromosomes are seen to be disposed upon the equatorial plate, and a polar view brings out the large number, estimated in other species to be over 100 (Burlingame 1907; Maheshwari and Singh 1934). Division II follows promptly upon completion of the first, and appears to be uniformly so inclined as to give rise to a quartet of tetrahedral spores. Cytokinesis is deferred until after division II. Certain apparent differences in size of the chromosomes are probably to be interpreted as due to overlaps; the small size of the chromosomes lends support to such a view. The mature spores retain the triradiate marking and have a finely papillate surface. Their diameter is 0.05 mm. and the wall is 3 μ in thickness.

Tapetum. The determination of the origin of this layer presents difficulties. When first distinguishable it consists of somewhat flattened rather deeply staining cells, more or less clearly in the same radial rows as sporogenous cells; mitoses however have not been observed. In later stages the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tapetal cells have increased in radial diameter and are distinctly more vacuolate than the sporogenous cells. It can then be seen that in certain cases the outer edge of the sporogenous mass of cells is uneven, a tapetal cell sometimes replacing a sporogenous cell (fig. 15). Again, what appear to be sister cells as evidenced by their position in radial rows are developed inwardly as sporogenous cells and outwardly as tapetum (fig. 21). This may be taken as evidence that the tapetal cells are potentially sporogenous. The thickness of the tapetum is from two to three layers. In figures 13 and 15 there is an appearance of a wall surrounding the sporangium; this is due to the collapse of inner jacket cells at the time of increase in volume of the sporangium, previously mentioned. Part of this increase is probably due to changes in shape, size, and number of the tapetal cells. These changes are going on quite actively while the sporogenous cells are giving rise to sporocytes, as is evidenced by the rather frequent mitoses visible in the tapetal layer (fig. 7). Some of the mitoses are completed, so far as the nuclei are concerned, giving rise to binucleate cells (figs. 8, 15), which are numerous if not indeed typical of this stage. Quadrinucleate cells also occur (fig. 16) but are distinctly less numerous than the binucleate ones. Some of the cells contain a single nucleus of spherical or irregular shape, measuring 30–34 μ in diameter instead of the 17–20 μ found in other tapetal cells (fig. 15). These observations indicate that in such cells the mitoses have been incomplete (fig. 11) or possibly that nuclear fusions have taken place. Figure 9 shows a particularly broad metaphase of width over 50 μ (cf. fig. 7); similar figures have been found showing the equatorial plate in face view, and these plainly indicate that the nuclei are heteroploid. No convincing appearances of amitosis have been found, but abnormal mitoses (fig. 10) sufficiently account for the diversity in size and shape of the nuclei. Steil (1935) has figured many similar cases in other members of the order, so that it is unnecessary to pursue the matter further than to refer to the frequency of such phenomena in our material.

The cells are now seen to have one or more large vacuoles, while the walls, heretofore distinct though thin, begin to melt away. In this way is produced a plasmodium which is presently seen occupying the spaces between the

Explanation of figures 15–21

FIG. 15. Medium stage of development of sporangium, showing the apparent wall, binucleate tapetal cells, and probably sterilized cells of potential sporogenous tissue, with normal sporocytes. ×200. FIG. 16. Sporangium at about the same stage as figure 15, with a quadrinucleate tapetal cell at left, and two binucleate cells at right. ×200. FIG. 17. General view of root, showing outer cortex, fungal layer, inner cortex, and part of stele with diarch xylem. ×70. FIG. 18. Young fertile spike with sporangia not yet showing tapetum. ×200. FIG. 19. Dividing sporocytes in plasmodium. Above is a metaphase, below this a telophase and a quartet. ×600. FIG. 20. Region of spike opposite a sporangium, where dehiscence takes place. "Wall" of sporangium, tapetum and sporogenous cells are also shown. ×120. FIG. 21. Tapetal cells in radial alignment with sporogenous cells. ×200.

"blocks" of sporocytes and later separating the individual spores (fig. 12). The plasmodium shows numerous vacuoles, also nuclei of various sizes and shapes which persist after the spore quartets are formed.

Shortly before the sporocytes are formed the edges of the spike show externally a series of slight depressions, one opposite each sporangium. In section the jacket cells are seen (fig. 20) to have divided periclinally in a more or less regular manner below each of the depressions. Later a transverse split appears at each of these points, setting free the spores. No other specialization connected with dehiscence can be seen.

DISCUSSION

Campbell (1911) came to the conclusion that in the Java material identified as *O. moluccanum* Schlect. there is no true "cauline" stele, basing his opinion on the observation that the vascular tissues are made up entirely of leaf traces and do not receive additions from the apical tissue of the stem. More recently Maheshwari and Singh (1934) observe with reference to *O. fibrosum* "there is no cauline stele; it is made up entirely of leaf traces." They mention moreover the presence of the commissure which is present at each leaf gap also in *O. palmatum*. It is worthy of remark that in each of these species there is a more or less tuberous rhizome (v. Campbell 1911, fig. 55; Maheshwari and Singh 1934, fig. 45). On the other hand, in the more slender rhizome of *O. Engelmanni* Prantl, material of which has been kindly supplied by Dr. E. P. St. John, I have observed a simple siphonostele with somewhat overlapping gaps from the edges of which two leaf traces arise. It would be possible to interpret the vascular system of the rhizome of *O. palmatum* as a congeries of leaf traces, but I prefer to follow Bower (1911, p. 281) in regarding the scattered condition of the stele as "a natural consequence of the parenchymatous swelling" which characterises this species as it does the other two mentioned previously. Attention may be drawn to the overlapping of characters in the three sections of the genus, such as the double leaf trace, the commissure, the different types of stele. As to the double leaf trace, which Bower (1911) considers a character in which *Ophioderma* and *Cheiroglossa* differ from all other Ophioglossaceae, it occurs not only in *O. Engelmanni*, a representative of *Euophioglossum*, but is seen in some of my preparations of *Botrychium dissectum*. Thus is emphasized the essential unity of the order.

The origin of the tapetum appears to vary in the three genera. Bower (1908) sums up the situation thus: "the large sporogenous mass of *Ophioglossum* throws off its superficial tissues as tapetum, . . . in the other two genera the tapetum originates from the adjoining tissue" (p. 457). The observations recorded in the present paper are in agreement with Bower's statement, and add an item to the list of features in which section *Cheiroglossa* is truly an *Ophioglossum*.

The shape of the mature tapetal cells varies from flat in *Botrychium* to irregularly cubical or polygonal in *O. palmatum*, and distinctly elongated radially in *Helminthostachys*.

As to the later stages in development of the tapetum, Steil (1935) was able by the use of satisfactory material of *B. virginianum* and *O. vulgatum* not only to find binucleate cells, which were lacking in the material used by Burlingame (1907) and Maheshwari and Singh (1934), but to furnish evidence for deriving these from incomplete or abnormal mitosis rather than amitosis. It is of interest to note that the tapetum of *O. palmatum* presents many stages closely resembling those figured by Steil and thus bears witness to the unity of the order in this regard. The presence of many tapetal nuclei dividing by mitosis, observed by Steil and now confirmed in the material of *O. palmatum*, goes far to dispose of the older theory which accounted for polynucleate tapetal cells by assuming amitosis. I have seen no cases in the Florida material that could not be explained on the basis of incomplete or abnormal mitosis.

Passing to the nature of the fertile spike, which is of course the central problem in the order, it would appear unnecessary to review the older theories, for several of these have been expressly relinquished by their supporters; and yet these theories have a way of gaining a new lease of life as a result of changing points of view or of more recent discoveries, for instance the adoption by Bower (1935) of the theory proposed in 1930 by Zimmerman, to the effect that the fertile spike represents a dorsi-ventral dichotomy of some ancient pteridophytic shoot. This case is the more interesting in view of the fact that Bower has entertained at least two other hypotheses: in 1908, etc., the strobilar nature of the *Ophioglossum* plant, and in 1926 the theory proposed by Roeper in 1859 to the effect that the fertile spike in *Botrychium* represents two fused basal pinnae.

It will readily be perceived that these three theories have entirely different starting points; for instance, what we may style the "dichotomy" view presupposes an origin for Ophioglossales quite early in the history of the megaphyll, while Roeper's theory of fusion assumes that the fern leaf was already existent before Ophioglossales branched off from the ancestral stock. It is at present not possible to exclude either of these possibilities, but it is well to bear in mind that the members of Ophioglossales which best illustrate a possible antero-posterior dichotomy are species of *Botrychium* of small size, usually regarded as reduced forms. I refer particularly to certain abnormal specimens of *B. simplex* Hitchc. in which large sporangia occur in both sterile and fertile segments. These could be interpreted as representing dichotomy in two planes, but their vascular as well as photosynthetic organs bear evidence of reduction. Other phases of this question are reserved for separate treatment.

The genus *Ophioglossum*, earlier considered primitive, is now regarded as the most advanced of the three genera, on the basis of venation, vascular structure, and sporangia. Within the genus, those species having a single spike are generally regarded as typical, while *O. palmatum* is accordingly an elaborated form showing duplication or chorisis (*pleiogeny* is the word Bower, 1911, suggests for such phenomena). It is possible, however, that this plant represents a form more nearly like the ancestral stock than do the other species, while the small species with unbranched sterile segment and single spike are reduced forms. Such a view is suggested though not explicitly stated by Eames (1936), and with this view I believe the balance of evidence is in accord. First, in *O. palmatum* the repeated dichotomy shown in juvenile stages and also in many adults appears like the persistence of a very ancient habit. The spikes with their truly lateral (marginal) position may represent specialized lobes, as was suggested in earlier papers (Chrysler 1910, 1911). Second, the venation does not show the specialization found in some of the smaller species. In the latter a more or less pronounced midvein is frequently visible in specimens which have been rendered translucent. A number of preparations illustrating this feature, also unpublished results, have most generously been put at my disposal by Dr. E. P. St. John. In *O. palmatum* on the other hand no such differentiation of veins can be made out. Moreover it has already been pointed out that the network is on a simpler plan, more suggestive of derivation from dichotomy, than is the case in some species of *Euopheoglossum*. Third, occasional cases of dichotomy are found in the sterile segment of small species. Fourth, a reduction series starting with *O. palmatum* duplicates the series which seems to be very probable in the genus *Botrychium*.

Against such a sequence may be urged the epiphytic habit in both of the large-leaved sections, *Ophioderma* and *Cheiroglossa*. Further, it is true that the arrangement of the fertile spikes is not very suggestive of dichotomy; much modification of the original condition is indicated, although the true marginal position of the spikes is probably significant. It seems certain, as is indicated on general grounds, that before *Botrychium* and *Ophioglossum* became separate genera the habit of fusion of the two basal lobes had already become settled.

Although the danger of introducing teratological evidence is admitted, it should be mentioned that the Florida material includes several spikes which are distinctly flattened, with a relatively broad thin lamina between the two rows of sporangia. Such cases may give us a glimpse of the appearance of the ancestral fertile lobes (fig. 4).

Another suggestion as to the possible appearance of the ancestral *Ophioglossum* comes from the remarkable genus *Trochopteris* (Bower 1926, p. 162), sometimes included under *Anemia*. In the leaf of this plant the basal

lobes bear sporangia in the marginal position. Recalling the morphology of the typical *Anemia* leaf, *Trochopteris* may well represent the persistence of an ancestral condition. The "monangial sorus" in Schizaeaceae may be indication of affinity with Ophioglossales, while the pronounced dichotomy in *Schizaea* marks the family as a primitive one, to which we may reasonably turn when seeking a parallel to the evolutionary history of Ophioglossales.

The most recent proposal concerning the morphology of the Ophioglossales is by Troll (1933), who has extended to this group his view of the peltate nature of the leaf of certain higher plants. He considers that *O. palmatum* best of all members of the order illustrates the peltate structure. He finds a parallel in the genus *Rodgersia* (Saxifragaceae), which would seem to be a rather advanced group in which to seek ancestral features. Moreover Troll admits having had no new material of *Ophioglossum* for study. He hazards the opinion that the cylindrical ("unifazial") structure of the petiole is so fixed that it no doubt occurs in sterile fronds as well as those which bear an adaxial spike. Unfortunately for the theory, my material has furnished an opportunity to test out this assumption, and I am in a position to say that in sterile leaves the vascular system of the petiole forms a C but the edges fail to close in to form an O; on the contrary the C opens out widely as soon as the rod-like petiole merges into the blade. It follows that Troll's schematic figure (1933, p. 570), explaining the plan of the leaf in *O. palmatum*, simply does not hold. Further, the evidence derived from abortive spikes proves nothing. This must surely be reasoning backwards, and is contradicted by the evidence from juvenile plants.

Most likely the occurrence of the strongly curved vascular system in the petiole of this plant is to be explained in terms of the mechanical necessities of a large heavy leaf, and we may interpret the C-shaped vascular system as a mere temporary "expedient" providing the necessary rigidity. If this is the correct interpretation we may go farther and suggest that the close approximation of the two edges of the C played a part in the evolution of a *single* spike in the adaxial position. The following stages are represented in the Florida material: (1) two basal spikes, closely approximated on the adaxial face of the petiole; (2) one adaxial (median) stalk which forks giving rise to two spikes; (3) the regular single basal spike supplied by a larger number of bundles than is the case in lateral spikes. In all of these cases the insertion of the spikes is really marginal, as is indicated by the vascular connections.

This short survey of theories leaves the writer with the idea that evidence for deriving Ophioglossales directly from plants which still had a primitive megaphyll, showing dichotomy in two planes, is still too scanty to be convincing, attractive as the general proposal appears. The evidence from *O. palmatum* and from more general considerations appears to favor the propo-

sition that the dorsiventral leaf had already appeared, but that dichotomy in one plane was still pronounced in the ancestors of the group.

SUMMARY

1. An adequate supply of suitably preserved material of *Ophioglossum palmatum* L. from Florida has made it possible to fill the chief gaps in our knowledge of the sporophyte.

2. The mycorrhizal condition is restricted to the root, where its occurrence is local.

3. The apical cell of the root has the usual tetrahedral form, with four cutting faces.

4. The development of spores and tapetum is traced. In the latter numerous binucleate cells and abnormal mitoses are found.

5. The lobing of the leaf is essentially dichotomous, as is seen in juvenile stages and in many mature individuals.

6. Venation is of a less advanced reticulate type than is shown in some species belonging to *Euophioglossum*.

7. The observations of Bower concerning the vascular plan of rhizome and petiole are confirmed.

8. It is held that the insertion of the fertile spikes is truly marginal. The lowest spike usually represents the fusion of two.

9. Evidence is adduced for the view that *O. palmatum* is nearer the ancestral condition than are the smaller species.

10. The overlapping of various features which have been used to distinguish the three subgenera of *Ophioglossum* indicates the essential unity of the genus.

11. Certain current theories as to the nature of the fertile spike are criticized in the light of recent observations.

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THE GENUS EVERARDIA

CHARLES GILLY

(WITH THREE FIGURES)

INTRODUCTION

During 1939, when identifying the specimens of Cyperaceae which Mr. G. H. H. Tate collected on Mount Auyan-tepui (5), I had occasion to examine the specimens which he brought back from earlier expeditions to Mount Roraima and Mount Duida. These included several unnamed specimens (numbers *469*, *542*, *720*, *721*, *800*, and *816*) provisionally referred to the genus *Everardia* by Britton (4).

It must be presumed, for several reasons, that Britton made only a casual inspection of these specimens. In the first place, I must disagree with his observation that these unnamed specimens are "not in good condition"; certainly complete vegetative portions of the plants, together with mature achenes and well-preserved anthers on almost every specimen, constitute excellent condition, especially in the Cyperaceae. Secondly, certain of these specimens were so different from the rest, and from the two known species in this genus, that the possibility of including them in *Everardia* seemed slight. Subsequent study showed that *Tate 720*, *721*, and *800* must be referred to the genus *Cephalocarpus* Nees. *Tate 542* is neither an *Everardia* nor a *Cephalocarpus*, although it does possess some characters of both genera; neither can it be placed in the rather closely related genus *Lagenocarpus* Nees. Probably this staminate specimen represents the only collection of an as yet undescribed genus.

Tate 426, from Mount Roraima, identified tentatively by Britton as *Everardia angusta* N. E. Br., is distinct from that species. *Tate 638*, also from Roraima, proves to be distinct from *E. montana* Ridley. *Tate 570*, provisionally referred to *Lagenocarpus rigidus* Nees in the Duida report (4), cannot be included in the genus *Lagenocarpus* but represents an undescribed species of *Everardia*. *Tate 469* and *816*, already mentioned, are conspecific and represent another undescribed species. These four new species, described in the present paper, together with *E. longifolia* from Mount Auyan-tepui (5), increase the number of species in this genus from two to seven.

In regard to the publication date of the genus *Everardia*, I quote a self-explanatory paragraph, signed by the Secretary of the Linnean Society of London, which precedes Oliver's paper on the im Thurn collections from Mt. Roraima (8): "Note.—The following determinations and descriptions of new plants were expressly drawn up for publication in the 'Transactions of the Linnean Society,' a confidential copy being given to Mr. E. F. im

Thurn to help him in writing the foregoing Introduction. During the delay required to prepare the accompanying Plates, Mr. im Thurn has taken the unprecedented course of printing the whole of the unrevised draft, at Demarara, in 'Timehri, the Journal of the Royal Agricultural and Commercial Society of British Guiana,' vol. v. pp. 145–233 (Dec. 1886), thus forestalling the present publication.—Sec. L. S." Because of Mr. im Thurn's "unprecedented course," it seems necessary to cite the publication of the genus *Everardia* Ridley as "in im Thurn, Timehri **5**: 210. Dec. 1886" (7), despite the fact that in the Index Kewensis the Timehri citation is relegated to brackets and preference given to "in Oliver, Trans. Linn. Soc. *Ser. II*, **2**: 287. July, 1887." The same consideration must also apply to the publication and citation of the species *E. montana* Ridley.

I quote from Ridley's generic description: "Stylus brevis, stigma *bifidum* lobis brevibus planis lanceolatis." And from his description of the species *E. montana:* "Stigma breviter *bifidum* lobis lanceolatis obtusis planis, violaceis." And, again, from his next succeeding paragraph: "This genus is most nearly allied to *Lagenocarpus*, but differs entirely from that genus, and from the rest of the Cryptangiae, in the lateral inflorescence, the *bifid* stigma, with short flat lobes, the absence of any cupule, and the presence of a large number of hypogynous bristles." (Except for the generic name, the italics in the preceding quotations are mine.) I do not know whether Ridley was merely careless in his diagnosis, or whether he happened to choose, for his examination, pistillate flowers from which one of the stigmas had been broken. It is sufficient to say that the remaining pistillate flowers on the type specimen distinctly show *three* stigmas, and the artist who made the drawings for plate 52 (8) portrayed *three* distinct stigmas in both of his delineations of the pistillate flower. I cannot agree, however, with either Ridley's description or the artist's portrayal of the shape of the stigmas. Ridley's comments are quoted above; the artist has shown the stigmas as little more than twice as long as wide, and as distinctly flattened-lanceolate in shape. My examination of the pistillate flowers of the four available specimens (the type included) of *E. montana* shows the stigmas to be linear, elongated and approximately terete, with, in some flowers, a very slight tendency toward inflation at the point of their separation from the style proper. The stigmas of the other six species of the genus are elongate and terete.

Examination of the achenes of the seven known species of this genus discloses that the "Setae hypogynae, copiosae, tortae" of Ridley (7), and the "pili hypogyni copiosi" of Brown (1), must be more fully explained. Even low magnification (×10) shows that the achenes of *Everardia* are seated in a hypogynous perianth cup formed by the marginal fusion of three minute scales, the free upper portions of which appear to be ciliate-mar-

gined. Higher magnification (×100) shows that these scales are formed of a single layer of unicellular hairs. The basal portions of these hairs are fused, thus forming the "scales," but above the area of fusion the individual hairs are free. The structure of these perianth scales is similar to those of the African genus *Microdracoides* Hua (2, 6) which may ultimately prove to be closely related to *Everardia*.

The arrangement of the inflorescence, as described by both Ridley and Brown, with staminate spikelets below and pistillate spikelets above, is borne out by the additional five species. The spikelets of the two sexes, however, are not wholly segregated. Occasional pistillate spikelets may be found at the apices of lower compound branchlets, or at the apex of the central branchlet arising from one or more of the lower inflorescence sheaths. Also, but not so frequently, occasional staminate spikelets are found on branchlets arising from the uppermost inflorescence sheaths.

The true stem (which in most Cyperaceae is very short) elongates from year to year. This stem should perhaps be termed an aerial rhizome, for, as it elongates by growth (the plant thus gradually becoming more and more top-heavy), "prop roots" are formed along its length. These "prop roots" force their way through the persistent leaf-sheaths which surround the stem and, after reaching the ground, aid in supporting the top-heavy plant. There seems to be no regular pattern, such as is exhibited by the axillary buds, for the formation of these "prop roots."

In his description of *E. angusta*, Brown (1) makes the statement: "Leaves in dense tufts of 3–6, distinct from the flowering culms . . ." An examination of the three available specimens (the type included) of *E. angusta* and of *Tate 426* from Mount Roraima explains this observation (by Brown). I have found that in this genus the leaves (as is typical of the entire family) are distinctly three-ranked, and that, at the point of attachment of the bases of their closed sheaths to the aerial rhizome, a distinct scar which encircles the rhizome in a closed band is formed. Between each scar and the next above—in the axil, therefore, of each leaf—is an axillary bud which sometimes remains dormant, sometimes produces an inflorescence, and sometimes develops into a branch of the rhizome. It was, undoubtedly, these young and few-leaved rhizome branches which Brown observed. Further to add to the illusion of distinct flowering culms and fascicled leaves, the flowering culm of the year seems always to be developed from the bud in the axil of about the sixth leaf below the growing tip of the rhizome.

For suggestions and advice on this problem, I wish to thank Dr. H. A. Gleason; and for his kindness in lending me the types and other available specimens of *E. angusta* and *E. montana*, I express my thanks to Sir Arthur W. Hill, Director of the Royal Botanic Gardens at Kew.

TAXONOMIC TREATMENT

Because of the discrepancies or omissions which I have already mentioned, and because of certain other points which have been observed in the study of the additional species, it seems necessary to emend the genus *Everardia* Ridley as follows:

EVERARDIA Ridley, in im Thurn, Timehri **5**: 210, 1886. Perennial, with an ascending, simple or branched, woody aerial rhizome surrounded by the persistent and more or less ragged sheath-bases of old leaves. Leaves rigid, more or less carinate, three-ranked, but sometimes appearing many-ranked. Flowering culms erect, leafless, axillary, basally enclosed by a short membranous sheath which is usually hidden within the leaf-sheath. Inflorescence composed of few–numerous tufts of erect, simple, or compound branchlets arising from the axils of close-fitting leafy-pointed sheaths. Spikelets monoecious, solitary at the apices of the branchlets. Lower portion of the inflorescence staminate or with 1–several pistillate spikelets at the apices of the compound branchlets or the central branchlet of a tuft or tufts bearing a solitary pistillate spikelet. Upper portion of the inflorescence wholly pistillate or rarely with 1–few staminate spikelets accompanying the pistillate. Staminate spikelets numerous, many-flowered; empty glumes 3–8, staminiferous 4–8; stamens under each staminiferous glume 6 (or rarely 4 or 8). Filaments capillary, persistent; anthers linear, two-celled, the connective prolonged between the loculi into a minute tuft of stiff hairs. Pistillate spikelets few and smaller than the staminate, 1-flowered, the ovary surrounded by 4–6 glumes. Achene from terete to obtusely-triangular, more or less conspicuously marked by 3 longitudinal carpellary lines, the apex tapering into a persistent, pubescent, or glabrous, conical, acute or truncated beak (style base), the body of the achene glabrous or pubescent. Style exserted, the stigmas 3, essentially terete, linear, elongated; style and stigmas conspicuously pubescent. Perianth cupular, formed by marginal fusion of 3 minute ciliate-margined scales, the scales frequently so reduced in size that the achene appears to be surrounded by a ring of hypogynous hairs; marginal hairs straight or twisted.

TYPE SPECIES: *E. montana* Ridley.

The genus *Everardia* belongs to the tribe Cryptangiae, the most closely related genera being *Cephalocarpus* and *Lagenocarpus*. Both *Everardia* and *Cephalocarpus* have axillary flowering culms and the perianth cup of three fused hypogynous scales; they may thus be distinguished readily from *Lagenocarpus* with its terminal inflorescence and lack of perianth. *Everardia* is easily separable from *Cephalocarpus*, the latter genus having capitate-condensed inflorescences and achenes with clavate, persistent beaks. *Everardia* has 6 stamens under each staminiferous glume of the staminate spikelets; both *Cephalocarpus* and *Lagenocarpus* have 2 stamens under each staminiferous glume.

Although Ridley published no formal dedication of the genus, the fact is obvious that *Everardia* is named in honor of Everard Ferdinand im Thurn (1852–1932), collector of the generic type specimen.

So far as is now known, the genus *Everardia* is restricted to the summits

of Mount Roraima, Mount Duida and Mount Auyan-tepui, but future exploration will undoubtedly discover the present known species and/or other species on other mountains in the Sierra Pacaraima complex. The accompanying map (fig. 1) shows the type localities of the species in this genus. It is of interest to note that, thus far, not one of the seven species has been collected from more than a single mountain.

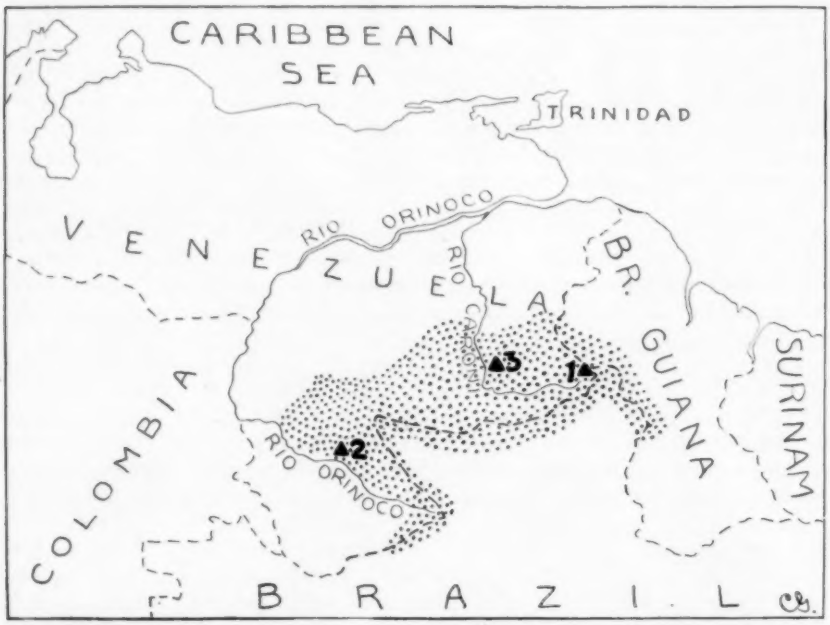

FIG. 1. Distribution of *Everardia*. 1. Mt. Roraima (*E. angusta, E. gracilis, E. montana*); 2. Mt. Duida (*E. glaucifolia, E. revoluta, E. duidae*); 3. Mt. Auyan-tepui (*E. longifolia*). General outline of the Sierra Pacaraima complex indicated by dotted area.

The specimens which I have examined in the study of this genus are deposited in the herbarium of the New York Botanical Garden (NY), and in the herbarium of the Royal Botanic Gardens at Kew (K).

KEY TO THE SPECIES

Leaves 4 mm. or less in width, folded for most of their length, thus appearing triangular in cross-section, thinly pilose on both surfaces and margins; beak of achene conical, longer than body of achene, densely stiff-pubescent.

Achene dark brown, both body and beak pubescent; perianth scales obovate; leaves 2–3.5 dm. long; flowering culm, inflorescence included, 3.5–5 dm. high.
1. *E. angusta*

Achene straw colored, the body glabrous and beak pubescent; perianth scales acute-triangular; leaves 0.7–1.5 dm. long; flowering culm, inflorescence included, 2–3 dm. high ..... 2. *E. gracilis*

Leaves more than 4 mm. in width, flattened, folded or with revolute margins (when folded, not appearing triangular in cross-section), the margins various but the leaf-surfaces not

pilose; beak of achene conical or truncated-conic, if longer than the body of the achene, then the beak glabrous or only minutely puberulent.

Flowering culm and inflorescence stiffly erect, considerably exceeding the leaves; leaves stiffly erect, the margins parallel for most of their length.

Leaves 4–6 mm. wide, 1.5–4 dm. long, thin, green, glabrous, with prominent midrib; staminate spikelets 7–11 mm. long, sterile glumes brown, oblong, bifid at apices, the green midrib extended between the teeth into a mucro 1.5–2.5 mm. long ..... 3. *E. longifolia*

Leaves 12–14 mm. wide, about 5 dm. long, thick, leathery, white-glaucous on both surfaces, the midrib obscure or almost obsolete; staminate spikelets 3.5–4 mm. long; sterile glumes purple-brown, broadly ovate to ovate-lanceolate, short mucronate but not bifid at apices ..... 4. *E. glaucifolia*

Flowering culm and inflorescence laxly ascending or more or less erect, scarcely exceeding the leaves; leaves reflexed or recurved, broadest at base and gradually tapering toward apices.

Leaves conspicuously revolute, appearing hollow-terete in cross-section, the margins smooth; achene light brown, the tricarpellary markings distinct; beak of achene slender, conical, half as long as body of achene. ..... 5. *E. revoluta*

Leaves folded or flattened, the margins ciliate or sharp-scabrous; achene dark brown, the tricarpellary markings faint; beak of achene conical and as long as achene body or bluntly truncated-conic and equalling or shorter than achene body.

Sheaths of inflorescence glabrous except for scanty pubescence at their mouths; beak of achene conical; leaves 10–15 mm. wide at base, folded at base, smooth and glabrous except for the white-ciliate margins; flowering culms stout, flattened ..... 6. *E. montana*

Sheaths of inflorescence densely minute-pubescent; beak of achene bluntly truncated-conic; leaves 5–8 mm. wide at base, flat for entire length, upper surface granular-roughened, the lower smooth and glabrous, the margins sharp scabrous; flowering culms capillary, subterete ..... 7. *E. duidae*

1. EVERARDIA ANGUSTA N. E. Brown, Trans. Linn. Soc. II, **6**: 73. 1901. *Cryptangium stamineum* N. E. Brown; Clarke, Kew Bull. Add. Ser. **8**: 135, nomen. 1908.[1]

Aerial rhizome simple or branched, 2–3 mm. in diam., to at least 5 cm. long, surrounded by the ragged, fibrous, dark brown leaf-sheaths. Leaves 2–3.5 dm. long, 2–4 mm. wide, linear, acute, usually folded below, bicarinate above, appearing triangular in cross-section, more or less recurved, thinly pilose. Flowering culms strictly erect, flattened, slightly concave on one side, convex on the other, sparingly pilose to glabrate, about 1.5 mm. wide, including the inflorescence 3.5–5 dm. high; basal sheath 5–7 cm. long. Inflorescence 3.5–5 dm. high; basal sheath 5–7 cm. long. Inflorescence of 4–5 distant tufts of spikelets; sheaths dark brown, glabrous or thinly pilose, 8–20 mm. long, the leaf-like points about one-third longer than the sheaths. Staminate spikelets 7–8 mm. long, 2–2.5 mm. in diam.; sterile glumes 5–7, oblong, acute, mucronate, brown, thinly and minutely pubescent on the

[1] Pfeiffer (9, p. 44) states that the nomen nudum *Cryptangium stramineum* [sic!] N. E. Br., refers to this species. In my examination of the type specimen, I find the crossed-out name *Cryptangium*, in Brown's handwriting, above the name *Everardia angusta*. Following this is an erasure through which may be dimly seen "*stamineum*." It is indeed unfortunate that this cheironym was inadvertently published in Clarke's posthumous Cyperaceae paper.

back; staminiferous glumes 4–6, oblong, obtuse; stamens under each glume 6. Pistillate spikelets 6 mm. long, 1.5 mm. in diam.; glumes 5, oblong-lanceolate, acute, mucronate, minutely ciliate. Achene subterete, ovoid, pubescent, dark brown, 2–2.5 mm. long, about 1 mm. in diam., the tricarpellary markings distinct; beak persistent, long-conic, about 3 mm. long, densely covered with short, dark brown pubescence. Perianth scales obovate, about one-eighth as long as body of achene; marginal hairs copious, about half as long as body of achene. Stigmas linear, terete, dark brown. (Fig. 2, *a*, *a'*.)

For the sake of easier comparison between species, I have, above, amplified Brown's specific description. Also, I have changed his measurements into the metric system.

VENEZUELA—BOLIVAR: Mount Roraima, summit, autumn 1898, *McConnell & Quelch 676* (TYPE) (K); 2500 m., Jan., 1910, *E. Ule 8539* (K); summit, Nov. 26, 1927, *G. H. H. Tate 435* (NY).

2. **Everardia gracilis** Gilly, sp. nov. Rhizomata breviora, ramosa, 2 mm. diam. minusve, vaginis persistentibus atro-brunneis lacerato-fibratis tecta; folia 0.7–1.5 dm. longa, 2–4 mm. lata, linearia acuta bicarinata pilosa; culmi floriferi cum inflorescentia 2–3 dm. alti; vagina ad basim 2–3 cm. longa; spiculae masculae 6.5 mm. longae, 1.5–2 mm. diam.; spiculae foemineae 5 mm. longae, 1.5 mm. diam., glumae 5; achaenia subteretia ovoidea glabra straminea, 2.5–3 mm. longa, 1 mm. diam.; rostro pubescente, 3.5 mm. longo; squamellae hypogynae triangulares quam corpus achaenii 6-plo breviores; stigmata linearia teretia pallido-brunnea.

Aerial rhizome short, 2 mm. or less in diam., branched, surrounded and hidden by the persistent, ragged-fibrous, dark-brown leaf-sheaths. Leaves 0.7–1.5 dm. long, 2–4 mm. wide, linear, acute, folded below, strongly bicarinate above, appearing triangular in cross-section, more or less recurved, thinly pilose on margins and midrib. Flowering culms stiffly erect, subterete, sparingly pilose to glabrate, 1–1.5 mm. in diam., including the inflorescence 2–3 dm. high; basal sheath 2–3 cm. long. Inflorescence of 5 tufts of spikelets; sheaths dark brown, densely appressed-pubescent to glabrous, 5–18 mm. long, the leaf-like point as long as the sheath. Staminate spikelets 6.5 mm. long, 1.5–2 mm. in diam.; sterile glumes 4, oblanceolate, acute and mucronate, brown, thinly pubescent or glabrous; staminiferous glumes 4, oblong, rounded at apex; stamens under each glume 6. Pistillate spikelets 5 mm. long, 1.5 mm. in diam.; glumes 5, narrowly lanceolate, acute, minutely ciliate on the margins. Achenes sub-terete, ovoid, glabrous, straw-colored, shining, 2.5–3 mm. long, 1 mm. in diam., tipped by persistent beak about 3.5 mm. long, tricarpellary markings distinct; beak densely covered with crisp, golden-brown pubescence. Perianth scales equilaterally triangular, one-sixth as long as body of achene; marginal hairs rather scanty, about half as long as body of achene. Stigmas linear, terete, light brown. (Fig. 2, *b*, *b'*.)

VENEZUELA—BOLIVAR: Mt. Roraima, summit, Nov. 26, 1927, *G. H. H. Tate 426* (TYPE) (NY).

3. EVERARDIA LONGIFOLIA Gilly, in Gleason & Killip, Brittonia **3**: 153. 1939. Aerial rhizome simple, about 4 mm. in diam., surrounded by the persistent, dark brown, fibrous-reticulated leaf-sheaths. Leaves 1.5–4 dm. long, 4–6 mm. wide, stiffly erect, thin, green, glabrous, flattened for most of their

length, not folded below, the upper one-third or less bicarinate, margins and midrib minutely scabrous. Flowering culms stiffly erect, somewhat flattened, two-edged but not winged, slightly scabrous on the edges, 2–4 mm. wide, including the inflorescence 3.5–8 dm. high; basal sheath 2–3.5 cm. long. Inflorescence of 5 or more distant tufts of spikelets; sheaths brown, strongly-veined, glabrous, distinctly flattened and two-edged, 10–15 mm. long, the leaf-like points twice the length of the sheaths. Staminate spikelets 7–11 mm. long, 1.5–2.5 mm. in diam.; sterile glumes 5–7, brownish, oblong, obscurely 2-toothed at the apex, the green midrib extended between the teeth into a mucro 1.5–2.5 mm. long, glabrous except for sparse short-pubescence on upper margins and mucro; staminiferous glumes 4–5, lanceolate, acute to mucronate; stamens under each glume 6. Pistillate spikelets, which would be in the upper part of the inflorescence, not present owing to the condition of the specimens. Achene, therefore, unknown. (Fig. 2, *c*.)

VENEZUELA—BOLIVAR: Mt. Auyan-tepui, 2200 m., Dec. 1937, *G. H. H. Tate 1347* (TYPE) (NY).

4. **Everardia glaucifolia** Gilly, sp. nov. Rhizomata breviora, simplicia, 4–6 mm. diam., vaginis persistentibus nigro-brunneis fibro-laceratis tecta; folia ad 5 dm. longa, 12–14 mm. lata, crassa coriacea albo-glaucescentia erecta, margine superiore revoluto; culmi floriferi cum inflorescentia erecti, 7.5–9.5 dm. alti; vagina ad basim 2–3 cm. longa; spiculae masculae 3.5–4 mm. longae, 1.5 mm. diam., glumis vacuis 6–7, ovatis vel ovato-lanceolatis, ad apicem breviter mucronatis nec bifidis, glabris, glumis fertilibus 4–5, ovatis vel late lanceolatis acutis vel sub-truncatis; spiculae foemineae 2.5–3.5 mm. longae, 1–1.5 mm. diam., glumis 5–7; achaenia subteretia ovoidea glabra atro-brunnea, 2.5 mm. longa, 1.5 mm. diam.; rostro glabro truncato, corpus achaenii subaequante; squamellae hypogynae subrotundae, quam corpus achaenii 10-plo breviores, pilis quam lamina duplo longioribus tortis; stigmata atro-brunnea minute pubescentia.

Aerial rhizome very short, simple, 4–6 mm. in diam., surrounded by the persistent black-brown fibrous-ragged leaf-sheaths. Leaves about 5 dm. long, 12–14 mm. wide, thick, leathery, white-glaucous on both surfaces, stiffly erect, folded below, margins strongly revolute above, margins and mid-rib smooth, glabrous. Flowering culms stiffly erect, flattened, two-edged but not winged, glabrous or slightly roughened on the edges, including the inflorescence 7.5–9.5 dm. high; basal sheath 2–3 cm. long. Inflorescence of 7–10 distant tufts of spikelets; sheaths of the inflorescence terete, minutely appressed-pubescent on the prominent veins, brown or purple, 5–20 mm. long, the leaf-like points as long as the sheaths. Staminate spikelets 3.5–4 mm. long, 1.5 mm. in diam., numerous; sterile glumes 6–7, purple-brown, broadly ovate to ovate-lanceolate, short mucronate, not bifid at the apex, glabrous or nearly so; staminiferous glumes 4–5, ovate to broadly lanceolate, acute or sub-truncate, brownish with narrow, erose hyaline margins; stamens under each glume 6. Pistillate spikelets 2.5–3.5 mm. long, 1–1.5 mm. in diam.; glumes 5–7, broadly ovate-lanceolate, short mucronate, brown-purple with narrow erose hyaline margins. Achene subterete, ovoid, glabrous, dark brown, about 2.5 mm. long, 1 mm. in diam., tipped by a persistent, glabrous, truncated beak about as long as the body of the achene, the tricarpellary markings scarcely distinct. Perianth scales subrotund, one-tenth as long as the body of the achene, marginal hairs about twice as long as the scales, copious, twisted. Stigmas capillary, terete, dark brown, minutely pubescent. (Fig. 2, *d*, *d'*.)

VENEZUELA—TERRITORIO AMAZONAS: Mt. Duida, ridge northwest of Vegas Brook, 4400 ft., Jan. 1–4, 1929, *G. H. H. Tate 570* (TYPE) (NY).

5. **Everardia revoluta** Gilly, sp. nov. Rhizomata simplicia, 5 mm. diam., ad 10 cm. alta, vaginis persistentibus confertis atro-purpureo-brunneis rigidis coriaceis nec laceratis tecta; folia 1.5–3 dm. longa, ad 6–8 mm. lata

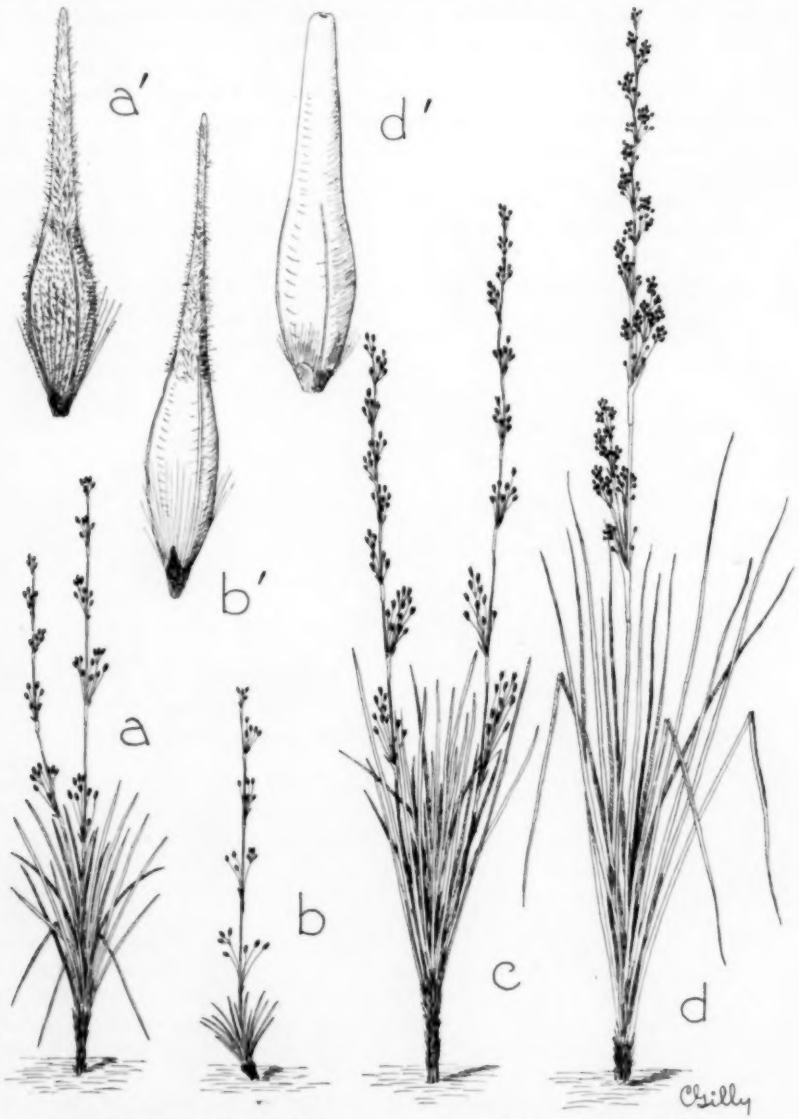

FIG. 2. *Everardia* (habit sketches $\frac{1}{3}$ natural size; achenes × 10). *E. angustata* N. E. Br.; *a*, habit, *a′*, achene (drawn from *Tate 435*). *E. gracilis* Gilly; *b*, habit, *b′*, achene (drawn from *Tate 426*). *E. longifolia* Gilly; *c*, habit, (drawn from *Tate 1347*). *E. glaucifolia* Gilly; *d*, habit, *d′*, achene (drawn from *Tate 570*).

ad basim, coriacea glabra, margine glabro inferne complanato supra medium valde revoluta; culmi floriferi laxe adscendentes vel erecti, cum inflorescentia 2–3.5 dm. alti; vagina ad basim 1 cm. longa; spiculae masculae 4–5 mm. longae, 1 mm. diam.; spiculae foemineae 3–3.5 mm. longae, 1 mm. diam., glumis 5, lanceolatis mucronatis glabris; achaenia teretia glabra pallide brunnea, 2–3 mm. longa, 0.6–1 mm. diam., rostro gracili glabro, quam corpus achaenii dimidio breviori; squamellae hypogynae minutae orbiculares, pilis copiosis tortis ciliatis; stigmata pallide brunnea.

Aerial rhizome simple, 5 mm. in diam., to at least 10 cm. high, surrounded by persistent, crowded, dark purple-brown, firm and coriaceous leaf-sheaths. Leaves 1.5–3 dm. long, about 6–8 mm. wide at the base, gradually tapering to the apex, leathery, flattened below, entirely glabrous, the margins smooth, entire, strongly revolute above the middle, the leaf appearing hollow-terete in cross-section. Flowering culms laxly ascending to erect, flattened, two-edged but not winged, 1.5–2 mm. wide, glabrous, including the inflorescence 2–3.5 dm. high; basal sheath about 1 cm. long, entirely hidden by the leaf-sheaths. Inflorescence of 5–8 tufts of spikelets; sheaths brown, glabrous, 5–20 mm. long, the leaf-like points slightly shorter than the sheaths. Staminate spikelets 4–5 mm. long, 1 mm. in diam., sterile glumes 4, lanceolate, mucronate, glabrous, light brown; staminiferous glumes 4–6, oblong, from acute to obtuse, margins minutely ciliate; stamens under each glume 6. Pistillate spikelets 3–3.5 mm. long, 1 mm. in diam.; glumes 5, lanceolate, mucronate, the midribs prominent, glabrous. Achenes terete, glabrous, light brown, tapering to both ends, 2–3 mm. long, 0.7–1 mm. in diam., tipped by the slender glabrous beak half as long as the body of the achene, the tricarpellary markings distinct. Perianth scales, minute, orbicular, the marginal hairs two-thirds as long as the body of the achene, copious, twisted. Stigmas linear, terete, long-exserted, light brown. (Fig. 3, *e*, *e'*.)

VENEZUELA—TERRITORIO AMAZONAS: Mount Duida, crest of ridge 25, 6300 ft., Nov. 26—Dec. 16, 1929, *G. H. H. Tate 469* (TYPE) (NY); Gorge of the Cano Negro, Savanna Hills, 4000 ft., 1928–1929, *G. H. H. Tate 816* (NY).

In addition to emending the generic description, and for much the same reasons, it has seemed necessary to emend the following species:

6. EVERARDIA MONTANA Ridley, in im Thurn, Timehri **5**: 210. 1886. Aerial rhizome simple, about 1 cm. in diam., surrounded by the persistent, dark brown, reticulate-fibrous leaf-sheaths. Leaves 1.5–1.8 dm. long, 10–15 mm. wide at base, tapering gradually to the apex, folded below, margins slightly revolute above, leathery, glabrous except for the shortly white-ciliate margins. Flowering culms laxly ascending or sub-erect, flattened, more or less concave on one side, slightly winged, the wings minutely ciliate, 2–3 mm. wide, including the inflorescence 2–2.5 dm. high; basal sheath 3–3.5 cm. long. Inflorescence of 7–8 tufts of spikelets; sheaths of the inflorescence dark brown, somewhat compressed, from minutely pubescent to glabrate, 5–20 mm. long, the leaf-like points slightly shorter than the sheaths. Staminate spikelets 5–7 mm. long, about 2 mm. in diam.; sterile glumes 3–4, brown, strongly veined, ovate-lanceolate, glabrous, short-mucronate, sometimes minutely bifid at the apices; staminiferous glumes 5–7, lanceolate, acute or truncate, sometimes minutely mucronulate, the margins minutely ciliate; stamens under each glume 6. Pistillate spikelets 4–5 mm. long, 1–1.5 mm. in diam.; glumes 5–6, lanceolate, purple-brown, from acute to more or less mucronate.

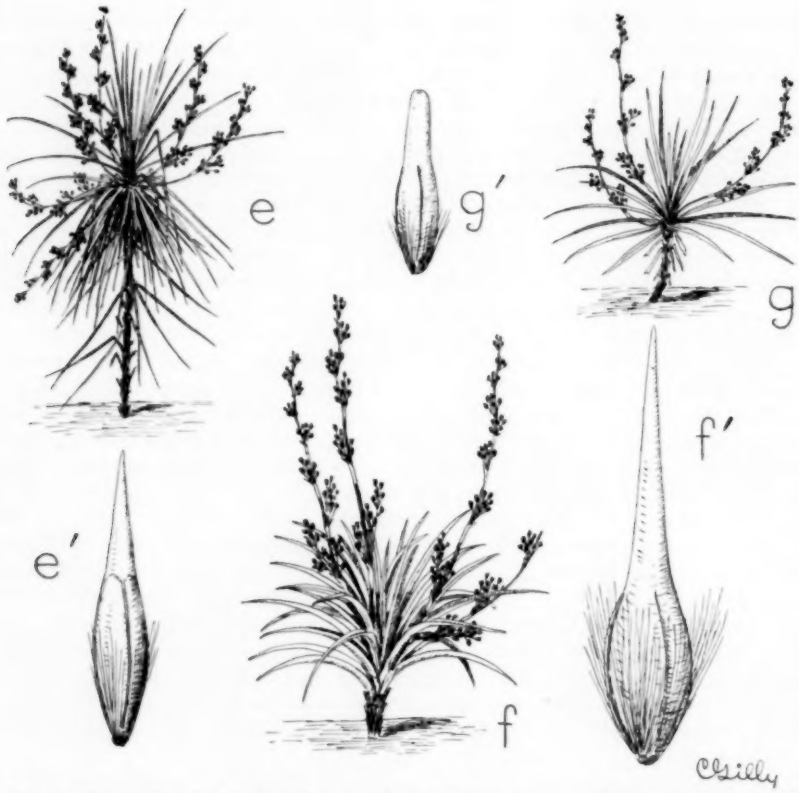

FIG. 3. *Everardia* (habit sketches $\frac{1}{8}$ natural size; achenes × 10). *E. revoluta* Gilly; *e*, habit, *e′*, achene (drawn from *Tate 469*). *E. montana* Ridley; *f*, habit, *f′*, achene (drawn from *Tate 438*). *E. duidae* Gilly; *g*, habit, *g′*, achene (drawn from *Tate 638*).

Achene ovoid, dark brown, the tricarpellary markings faint, 2–3 mm. long, 1–2 mm. in diam., glabrous, tipped by a slender, glabrous, light brown beak half again as long as the body of the achene. Perianth scales very minute, orbicular or truncate; marginal cilia copious, appearing as a hypogynous ring of hairs, twisted, as long as or longer than the body of the achene. Stigmas 3, linear, from sub-terete to terete, somewhat inflated at their junction with the style proper, dark purple-brown, minutely pubescent. (Fig. 3, *f*, *f′*.)

VENEZUELA—BOLIVAR: Mt. Roraima, the Ledge, Dec., 1884, *E. F. im Thurn 335* (TYPE) (K); summit, 8600 ft., autumn 1898, *McConnell & Quelch 674* (K); 2500 m., Dec., 1909, *E. Ule 8543*, (K); summit, Nov. 27, 1927, *G. H. H. Tate 438* (NY).

7. **Everardia duidae** Gilly, sp. nov. Rhizomata simplicia, 2–4 mm. diam., ad 10 cm. alta, vaginis nigro-brunneis lacerato-fibratis tecta; folia 1–1.4 dm. longa, ad basim 5–8 mm. lata, infra glabra, supra granulato-asperata, margine arguto scabro; culmi floriferi laxe adscendentes, cum inflorescentibus ad 1.5 dm. alti; vagina ad basim 1.5–2 cm. longa; vaginae inflorescentiae minute cano-pubescentes; spiculae masculae ad 4 mm. longae, 1–1.5 mm. diam.,

glumis vacuis 4–6, ovatis vel lanceolatis mucronatis supra medium minute-pubescentibus, glumis staminibus 5–8, lanceolatis acutis glabris; spiculae foemineae 3 mm. longae, 1–1.5 mm. diam., glumis 5–6; achaenia glabra atro-brunnea, 1.2–1.7 mm. longa, 0.5 mm. diam.; rostro glabro truncato, corpus achaenii subaequante; squamellae hypogynae minutae orbiculares, ciliis paucis, quam corpore achaenii dimidio brevioribus.

Aerial rhizome simple, 2–4 mm. in diam., to at least 10 cm. tall, surrounded by blackish, ragged-fibrous leaf-sheaths. Leaves 1–1.4 dm. long, 5–8 mm. wide at the base, tapering gradually to the apex, glabrous on the under surface, granular-roughened above, flat for most of their length, slightly bicarinate at apex, margins sharp-scabrous, almost saw-edged. Flowering culms laxly ascending, flattened, densely appressed-pubescent, about 0.5 mm. wide, including inflorescence about 1.5 dm. high; basal sheath 1.5–2 cm. long. Inflorescence of 5–6 tufts of spikelets; sheaths of the inflorescence dark-brown, minutely hoary-pubescent, 4–10 mm. long, the leaf-like points as long as the sheaths. Staminate spikelets about 4 mm. long, 1–1.5 mm. in diam.; sterile glumes 4–6, from ovate to broadly lanceolate, mucronate, minutely pubescent above the middle; staminiferous glumes 5–8, lanceolate, acute, glabrous; stamens under each glume 4–8. Pistillate spikelets 3 mm. long, 1–1.5 mm. in diam., the glumes 5–6, ovate to lanceolate, mucronate, minutely pubescent to glabrate. Achene 1.2–1.7 mm. long, 0.5 mm. in diam., glabrous, dark brown, tapering into a blunt-truncated beak about as long as the body of the achene; beak glabrous, or sometimes minutely puberulent at the apex. Tricarpellary markings faint. Perianth scales minute, orbicular; marginal hairs few, about one-half as long as the body of the achene, straight or somewhat twisted. Stigmas linear, dark brown. (Fig. 3, *g*, *g'*.)

VENEZUELA—TERRITORIO AMAZONAS: Mt. Duida, summit of peak 7, 7100 ft., 1928–1929, *G. H. H. Tate 638* (TYPE) (NY).

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STUDIES ON AMERICAN HEPATICAE—I. REVISION OF THE GENUS THYSANANTHUS

MARGARET FULFORD

(WITH FIFTY-ONE FIGURES)

Three species of *Thysananthus*, a genus of the subgroup Holostipae of the Lejeuneae, have been reported from the Americas and a fourth is here proposed as new. Spruce[1] has described several species under *Lejeunea*, subgenus VIII, *Thysano-Lejeunea*, namely *L. amazonica* from the Amazon country, *L. dissoptera* from Guiana, and *L. pterobryoides* from Ecuador. In addition to these, Nees von Esenbeck[2] described a plant from Jamaica as *Phragmicoma Lehmanniana*, which Stephani later transferred to *Thysananthus*. Verdoorn[3] suggested that this plant was a *Caudalejeunea*. An examination of a portion of the type material shows that it is identical with *Caudalejeunea Lehmanniana* (Gottsche) Evans[4] and it should therefore be reduced to synonymy. Taylor[5] described plants collected in Ecuador by Professor W. Jameson under the name *Thysananthus mexicanus*. His plants do not have the characteristics of the genus *Thysananthus* as it has been delimited by recent monographers so that the species is a member of some other genus of the Lejeuneae.

The genus[6] as understood by Evans,[7] Verdoorn,[3] and others may be characterized as follows: the female inflorescence is terminal on the main stem or principal branch, with innovations proceeding from one or both sides below; the perianth is 3-angled in transverse section, with the ventral keel sharp and distinct; there are no secondary folds or ridges; carinal and surface wings are developed in some species; the female bracts and bracteoles, and the keels of the perianth are toothed to a greater or lesser degree; and the leaves and underleaves usually show some indications of teeth along the margins, particularly in the apical region.

The plants are large and grow in depressed mats or among other bryophytes on the trunks and bases of trees and over logs. The stem is robust and

[1] Hepaticae of the Amazon and Andes. Trans. Bot. Soc. (Edinburgh) **15**: 105–110. 1884.

[2] In Gottsche, Lindenberg & Nees von Esenbeck, Syn. Hep. 302. 1845.

[3] Die Frullaniaceis XV. Die Lejeuneaceae Holostipae der Indomalaya unter Berücksichtigung sämtlicher aus Asien, Australien, Neu-seeland und Ozeanien angeführten Arten. XIII. *Thysananthus*. Ann. Bryol. Supl. **4**: 163–188. 1934.

[4] Hepaticae of Puerto Rico VIII. *Caudalejeunea*. Bull. Torrey Club **34**: 554–557. pl. 33, fig. 1–12. (1907.) 1908.

[5] On some new Musci collected by Professor W. Jameson on Pichincha. Hooker's Jour. Bot. **7**: 187–199. 1848.

[6] For synonymy in the genus *Thysananthus* see Verdoorn, l. c.

[7] Hepaticae of Puerto Rico VIII. *Symbiezidium, Marchesinia, Mastigolejeunea, Caudalejeunea* and *Bryopteris*. Bull. Torrey Club **34**: 533–568. *pl. 31–33*. (1907.) 1908.

is differentiated into a prostrate primary caudex which is appressed to the substratum, and ascending or upright secondary stems which are usually abundantly branched. The branches are olive or dark green and often become deeply pigmented with brown.

Evans[8] describes the secondary stem of *T. amazonicus* as being 3–8 cm. in length and about 0.15 mm. in diameter. The transverse section shows a uniform orange-brown pigmentation except for the slightly darker middle lamellae. The cortex is made up of 30–33 rows of thick-walled cells ranging from 10 to 20 μ in width, and from 10 to 15 μ in thickness. The cells of the medulla are quite similar, except that they have distinctly larger cell-cavities, so that the medulla appears somewhat more open than the cortex.

The branching of the subfloral innovations, other vegetative branches, and the male branches seem always to be of the *Radula* type.[9]

The lobule is small in proportion to the lobe. The keel is rounded and the upper edge, which is entire, tends to be tightly appressed to the lobe, so that a definite, inflated water-sac is usually formed. The apical tooth is from one to seven cells long and may be curved.

Although the genus, as indicated by the stem structure, is clearly a member of the Holostipae, which are characterized by entire underleaves, several species have retuse or distinctly bifid underleaves. Three of the American species show this characteristic. The additional generic characteristics are discussed under the descriptions of the separate species.

The writer wishes to acknowledge the helpful criticism of Dr. A. W. Evans of Yale University, and the courtesies extended by the New York Botanical Garden during the preparation of this paper.

The following abbreviations have been used to designate the location of specimens in the citations under the individual species: M, Missouri Botanical Garden; NY, New York Botanical Garden; and Y, Herbarium of Yale University, including the private collection of Dr. A. W. Evans.

KEY TO THE SPECIES

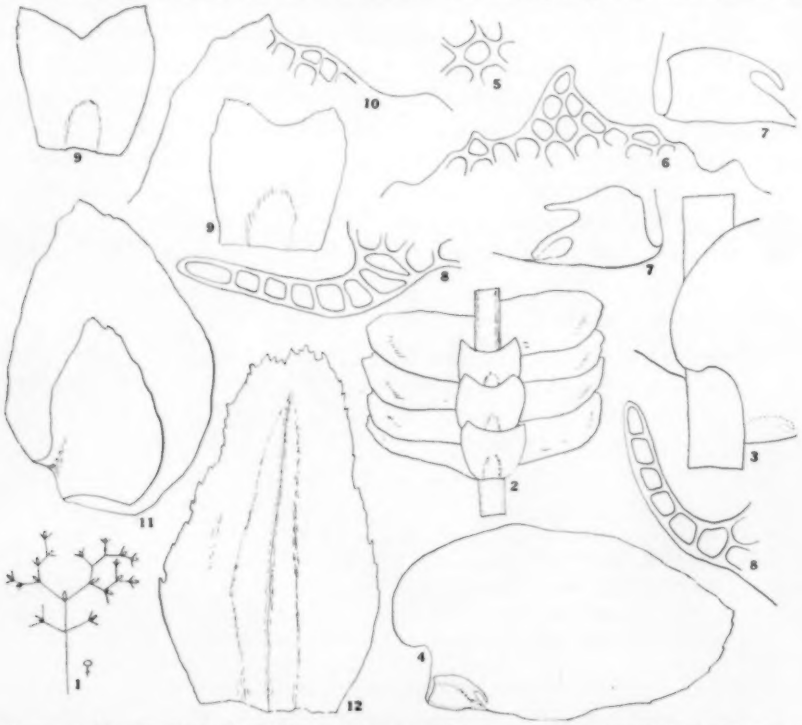
1. Underleaves obovate, rarely truncate, the apical margin serrate ..... 4. *T. comosus*
1. Underleaves subquadrate-cuneate, from retuse to deeply bifid.
   2. Lobule oblong, the tooth if present of only one or a few cells; leaf cells elliptical-angular in outline ..... 3. *T. amazonicus*
   2. Lobule more or less subquadrate, the tooth long, curved, of 5–7 cells; leaf cells quadrate in outline; underleaves distinctly bifid.
      3. Margins of the leaves and underleaves dentate with coarse teeth ..... 2. *T. pterobryoides*
      3. Margins of the leaves and underleaves from obscurely dentate to denticulate ..... 1. *T. Evansii*

[8] Anatomy of the stem in the Lejeuneae. Bull. Torrey Club **62**: 187–214; 259–280. *8 fig.* 1935.

[9] For a description of the various types of branching see Evans, Branching in the Leafy Hepaticae. Ann. Bot. **26**: 1–37. *36 fig.* 1912.

Thysananthus Evansii Fulford, sp. nov. Caules robusti, olivacei, pinnate ramosi, feminini dichotomi; folia imbricata, divaricata, ovata, 1–1.3 mm. longa, superne obscure serrata, cellulis 8–10 μ diam., lobulo parvo, dente apicali longo; foliola imbricata, subquadrato-cuneata, bifida; flores dioici; bracteae femininae foliosae, lobulis magnis, planis, ovatis, bracteola magna, ovata, carinata, crasse dentata.

Plants robust, olive-green, becoming darker green in the older portions: secondary stems stout, to 4 cm. or more in length, with leaves to 2 mm. broad, ascending, irregularly pinnate, the branches obliquely spreading, the female branch system showing apparently regular dichotomy: leaf insertion curved in the upper part; the leaves imbricated, spreading, becoming a little deflexed when dry, unsymmetrically ovate, 1–1.3 mm. long, 0.5 mm. broad at the base, obscurely serrate above the middle, the dorsal base cordate, the ventral margin straight; the lobule small, inflated, ovate, 0.12 mm. long, 0.1 mm. high, the free margin entire, appressed, the apical region of the lobe 8–10 μ in diameter, cells of the base much longer, a vitta not differentiated, the cell walls uniformly thickened, the cell lumina rounded, trigones not evident, the



FIGS. 1–12. *T. Evansii* Fulford. FIG. 1. Diagram of the branching pattern of a female plant. FIG. 2. Portion of a plant, ventral view, × 15. FIG. 3. Portion of a leaf and stem, dorsal view, × 30. FIG. 4. A leaf, × 30. FIG. 5. A cell from the apical portion of a leaf, × 400. FIG. 6. Outline of the apical margin of a leaf, × 300. FIG. 7. Lobules, one of them has developed two apical teeth, × 90. FIG. 8. Apical teeth of lobules, × 400. FIG. 9. Underleaves, × 30. FIG. 10. Outline of the apical margin of a tooth of an underleaf, × 300. FIG. 11. Female bract, × 30. FIG. 12. Female bracteole, × 30. Drawn from the type material.

cuticle smooth to faintly verruculose: underleaves imbricated, attached in a straight line, subquadrate-cuneate, 0.7 mm. long, 0.5–0.6 mm. broad in the upper part, retuse or bifid to one-fifth the length, the broad and pointed divisions and the obtuse to lunulate sinus serrate, the lateral margins convex, entire, the cells as in the leaf: dioicous: female branches short, on the main stem or branches, always subtended by two subfloral innovations, a pair of leaves below the involucre intermediate in form between the bracts and the normal leaves; the bracts leaf-like in outline, 1 mm. or more long, the margins often more strongly serrate than in the leaf, the lobule ovate, much enlarged, plane, mostly 0.7 mm. long, the apical tooth not evident; the bracteoles broadly ovate, 1.3 mm. or more long, the margin coarsely dentate, the apex obscurely bifid, keeled nearly to the apex, the angle broad: male branches, perianths and sporophytes not seen.

Habitat: On bark of trees, lowland forests.

Distribution: BRITISH HONDURAS: Punta Gorda, without collector's name, TYPE (M).

The distinguishing characteristics of the species are its olive-green color and dichotomously branched female stems; the long, curved tooth of the lobule of the leaf; the bifid underleaves serrate above the middle; and the long, keeled, more or less bifid, dentate, female bracteoles. See figures 1–12.

THYSANANTHUS PTEROBRYOIDES (Spruce) Stephani, Spec. Hep. **4**: 786. 1912. *Lejeunea* (*Thysano-Lejeunea*) *pterobryoides* Spruce, Trans. & Proc. Bot. Soc. Edinb. **15**: 109. 1884. *Bryopteris Wallisii* Stephani, Hedwigia **24**: 89. *pl. 1, fig. 1–8*. 1885. *Thysanolejeunea pterobryoides* Stephani (syn.), Spec. Hep. **4**: 786. 1912.

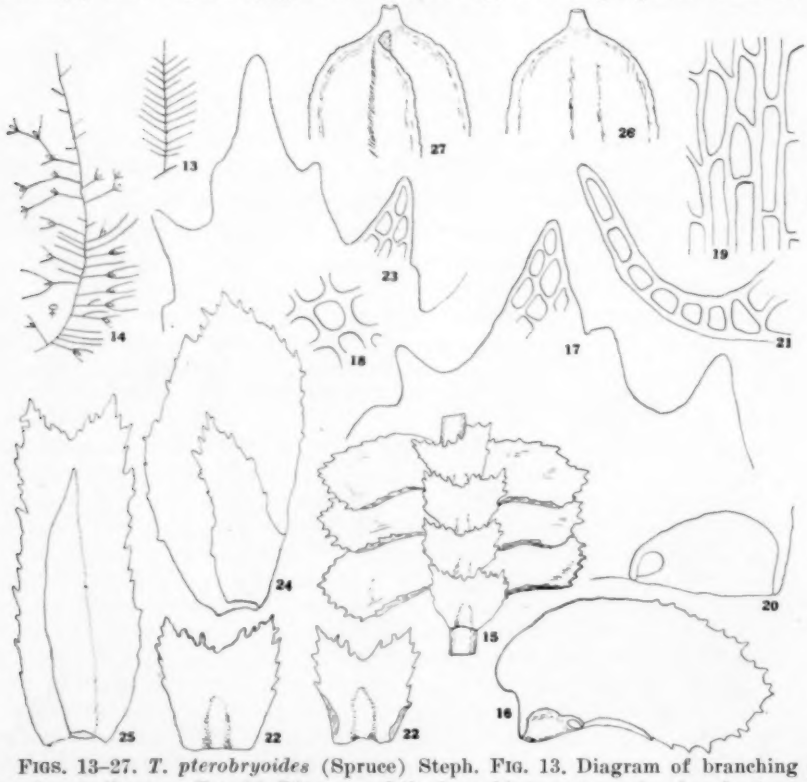
Plants olive green, becoming darker green in the older portions: secondary stems to 8 cm. or more in length, with leaves 2 mm. broad, ascending, more or less regularly and simply pinnate when sterile, inflorescences produced on primary branches of pinnate branch systems; leaf insertion curved in the upper part; the leaves imbricated, spreading, becoming a little deflexed when dry, 1–1.3 mm. long, 0.4–0.6 mm. broad at the base, unsymmetrically ovate, coarsely dentate above the middle, the dorsal base cordate, extending across the stem and beyond, the ventral margin more or less recurved, entire, the lobule inflated, ovate, 0.7–0.12 mm. long, 1.8–0.1 mm. high, the free margin appressed, entire, the apical tooth five to seven cells long, curved, the sinus deep, lumulate; the cells of the lobe averaging 8–10 μ in diameter, those of the basal area longer, a vitta not differentiated, the cell walls uniformly thickened, the cell lumina rounded, trigones not evident: underleaves imbricated, attached in a straight line, coarsely dentate, subquadrate-cuneate, 0.56–0.7 mm. long, 0.5–0.63 mm. broad in the upper part, bifid to one-fourth the length, the sinus lunulate, the teeth broad, acute, the cells as in the leaf: dioicous: female branches short, always with two subfloral innovations, a pair of leaves below the involucre intermediate in form between the bracts and normal leaves; bracts leaf-like in outline, to 1.3 mm. or more long, the lobule lanceolate, plane, more than half the length of the lobe, the apical tooth not evident, the lobe and lobule coarsely dentate above the middle; the bracteole oblong, to 1.5 mm. in length, bifid and coarsely toothed above the middle as in the underleaf, keeled nearly to the apex, the

angle acute: perianth to 2.5 mm. long, the keels sharp, crenulate, occasionally serrate, the beak short: male branches and sporophytes not seen.

Habitat: On bark of trees in forests.

Distribution: COSTA RICA: San José, Lehmann, cited by Stephani.[10] PANAMA: Island of Coiba, *Seemann* (Y, NY). COLOMBIA: Cordoba, *Killip 11776, 11801* (Y, NY); without locality, *Wallace* (NY). ECUADOR: Pastaza River, *Spruce 1885, 109;* Manabi, *Wallis,* cited by Stephani (1885, 89), TYPE of *Bryopteris Wallisii.*

The distinguishing characteristics of the species are its olive-green color, the simply and regularly pinnate branching, the long apical tooth of the



FIGS. 13–27. *T. pterobryoides* (Spruce) Steph. FIG. 13. Diagram of branching pattern of a sterile stem. FIG. 14. Diagram of the branching pattern of a female stem. FIG. 15. Portion of a plant, ventral view, ×15. FIG. 16. A leaf, ×30. FIG. 17. Outline of the apical margin of a leaf, ×300. FIG. 18. A cell from the apical portion of a leaf, ×400. FIG. 19. Cells from the basal portion of a leaf, ×300. FIG. 20. A lobule, ×90. FIG. 21. An apical tooth of a lobule, ×400. FIG. 22. Underleaves, ×30. FIG. 23. Outline of the apical margin of a tooth of an underleaf, ×300. FIG. 24. Female bract, ×30. FIG. 25. Female bracteole, ×30. FIG. 26. Upper portion of a perianth, dorsal view, ×30. FIG. 27. Upper portion of a perianth, ventral view, ×30. Drawn from material collected by Dr. Killip in Colombia.

[10] In Cryptogamae Centrali-Americanae. Hepaticae. Bull. Herb. Boiss. 2: 402–403. 1894.

lobule of the leaf, the bifid underleaves, and the coarsely dentate margins of the leaves and underleaves. See figures 13–27.

T. pterobryoides and *T. Evansii* have many characters in common, namely the color and size of the plants, the size of the leaves and underleaves, the size and shape of the leaf cells, the lobules of the leaves, and the production of pairs of subfloral innovations subtending the female inflorescences. They differ in that in *T. pterobryoides* the secondary stems are often very long, the branching is simply and regularly pinnate, and the female inflorescences are produced on primary branches of a pinnate branch system, while in *T. Evansii* the branches are less regularly pinnate and not so long, and the female plants always show an apparently regular dichotomy. (Compare figs. 13, 14 with fig. 1.)

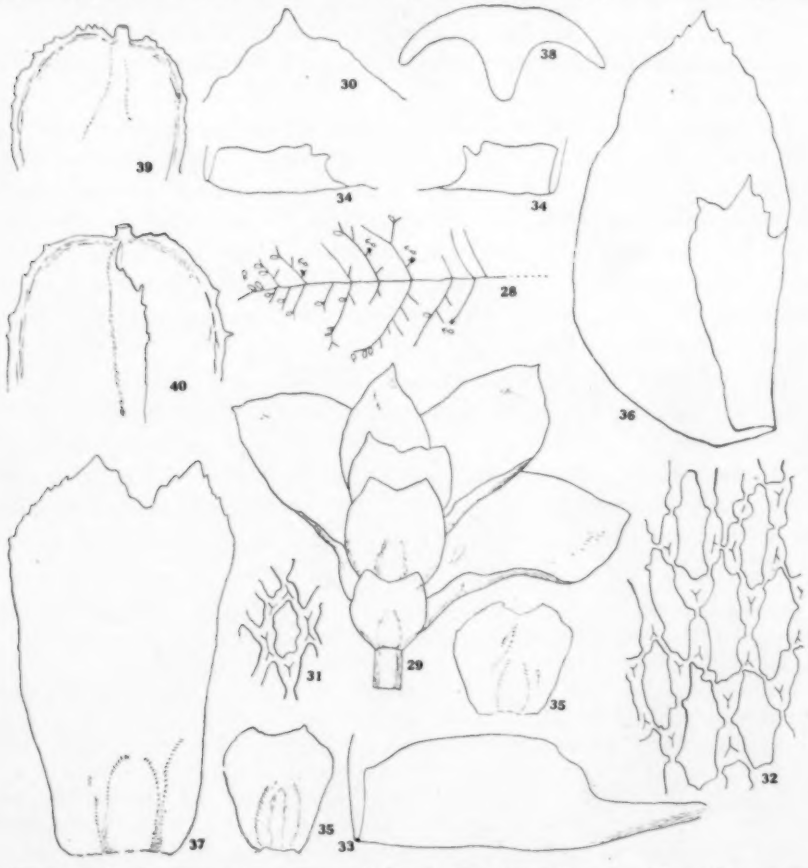
The margins of the leaves and underleaves, and the female bracts and bracteoles of the two are strikingly different. (Compare figs. 15, 16, 17, 22–25 with figs. 2, 4, 6, 9, 10–12.) The shape of the female bracts is quite similar in the two species, but the bracteoles of *T. Evansii* are broadly ovate and the angle of the keel is broad, while in *T. pterobryoides* the bracteoles are oblong and the angle of the keel is acute. Unfortunately no perianths have been found in *T. Evansii*, so that a comparison of this structure in the two species cannot be made at this time.

Not only do *T. pterobryoides* and *T. Evansii* have many characteristics in common but they also make up a unit within the genus which is different not only from the other South American forms but also from any of the Asiatic species with which I am familiar. All the other species have a deep brown pigmentation and have large leaf cells which are more or less elongate and hexagonal or angular-elliptical in outline, with conspicuous trigones, and often additional intermediate thickenings.

THYSANANTHUS AMAZONICUS (Spruce) Stephani, Spec. Hep. **4**: 784. 1912. *Lejeunea* (*Thysano-Lejeunea*) *amazonica* Spruce, Trans. Bot. Soc. Edinb. **15**: 106. 1884. *Thysanolejeunea amazonica* Stephani (syn.) l.c.

Plants dark greenish brown, becoming very dark brown in the older portions; secondary stems coarse, 6 cm. or more in length, with leaves to 3 mm. broad, irregularly pinnate, the branches oblique, often branched, female branches with only one subfloral innovation: leaf insertion curved in the upper parts; the leaves imbricated, spreading, tightly appressed to the stem when dry, averaging 1.4–1.6 mm. long, 0.8 mm. broad at the base, unsymmetrically ovate, entire except for an occasional serration, the dorsal base cordate, covering the stem and extending beyond, the ventral margin entire, recurved; the lobule small, inflated, oblong in outline, 0.3–0.42 mm. long, 0.15 mm. high, the free margin entire, appressed, the apical tooth sometimes evident, of one or two cells, the slime papilla not seen, the sinus shallow, lunulate; cells of the marginal and apical region and of the lobule 16–20 $\mu \times 8$ μ, those of the base longer, a vitta not differentiated, the cell walls thin, the trigones conspicuous, with convex sides, soon becoming confluent through the deposition of secondary material, intermediate thickening frequent, the cell lumina

angular-oblong in outline, the cuticle smooth to verruculose: underleaves imbricated, attached in a straight line, cuneate, retuse to shortly bifid, averaging 0.77 mm. long, 0.7 mm. broad in the upper part, the teeth very short and broad, the sinus shallow, lunulate, the margins entire, sometimes obscurely serrate on underleaves near the tip of the stem, the cells as in the leaf: autoicous: male inflorescences terminal on short lateral branches, the bracts in two to four pairs, at the tip of a branch, imbricated, the lobe broadly ovate, the lobule ovate, smaller, the apical tooth conspicuous, the margins sparsely dentate; the bracteoles imbricated, similar to the underleaves; antheridia in pairs: female branches short, occurring singly or several approxi-



FIGS. 28–40. *T. amazonicus* (Spruce) Steph. FIG. 28. Diagram of branching pattern of a stem. FIG. 29. Portion of a plant, ventral view, ×15. FIG. 30. Portion of the apical margin of a leaf, ×30. FIG. 31. A cell from the apical portion of a leaf, ×400. FIG. 32. Cells from the basal portion of a leaf, ×300. FIG. 33. Lobule, ×90. FIG. 34. Lobules, ×30. FIG. 35. Underleaves, ×15. FIG. 36. Female bract, ×15. FIG. 37. Female bracteole, ×15. FIG. 38. Outline of a cross section of the perianth. FIG. 39. Upper portion of a perianth, dorsal view, ×30. FIG. 40. Upper portion of a perianth, ventral view, ×30. Drawn from type material.

mate, appearing lateral, a subfloral innovation from only one side, the bracts similar in outline to the leaves, averaging 2 mm. long, the lobule oblong, ovate, plane, 0.8 mm. long, the margins of both coarsely toothed in the upper part; the bracteole oblong, bifid, 1.6 mm. or more in length, averaging 0.9 mm. broad in the upper part, the teeth broad, acute, the sinus acute, the margins of the teeth serrate and coarsely dentate: perianth to 2 mm. long, the beak short, the keels serrate and dentate with scattered teeth: sporophyte not seen.

Habitat: On bark of trees in forests.

Distribution: TRINIDAD: Mora Forest, *E. G. Britton 2878* (Y, NY); without locality, *Fendler* (NY). COLOMBIA: Without locality, *Wier* (NY). BRAZIL: Pará, Spruce, Hepat. Spruc., TYPE (Y, NY). BRITISH GUIANA: near Bartica, *Richards 188, 510* (Y).

The distinguishing characteristics of the species are the large, coarse, irregularly branched, dark greenish brown stems; the large, ovate, entire leaves with oblong lobules which have a 1–3-celled apical tooth; the long-angular cell lumina, large trigones and intermediate thickenings; and the large cuneate underleaves which are retuse or somewhat bifid at the apices. See figures 28–40.

T. amazonicus is readily distinguished from the preceding species because of its autoicous inflorescence, the deep brown pigmentation, the entire margins of the leaves and underleaves, the short apical tooth of the lobule, and the angular-oblong outline of the leaf cells.

THYSANANTHUS COMOSUS Lindenberg, in Lehmann Pug. Pl. **8**: 25. 1844. *Lejeunea comosa* Mitten, Jour. Linn. Soc. Bot. **5**: 109. 1861. *Lejeunea* (*Thysano-Lejeunea*) *comosa* Spruce, Trans. Bot. Soc. Edinb. **15**: 108. 1884. *Thysananthus dissopterus* Stephani, Spec. Hep. **4**: 784. 1912. *Thysanolejeunea dissoptera* Stephani (syn.) l.c.

Plants dark greenish brown, becoming very dark brown in the older portions; stems coarse, 5 cm. or more in length, with leaves to 2.5 mm. broad, irregularly pinnate or bipinnate, microphyllous branches frequent, female branches with only one subfloral innovation: leaf insertion curved in the upper part; the leaves imbricated, spreading, ascending and appressed to the stem when dry, averaging 1.4 mm. long, 0.85 mm. broad at the base, unsymmetrically ovate, entire except for an occasional serration, the dorsal base cordate, covering the stem and extending beyond, the ventral margin entire, recurved: the lobule small, inflated, ovate in outline, 0.3–0.4 mm. long, 0.2 mm. high, the free margin entire, appressed, the apical tooth one to several cells long, the inner (proximal) tooth sometimes evident, of one or two cells, the sinus very shallow; cells of the lobule and the margin and apical regions averaging 20 μ long, 12 μ wide, those of the base longer, a vitta not differentiated, the cell walls thin, the trigone conspicuous, with convex sides, often becoming coalesced, intermediate thickenings frequent, the cell lumina angular-oblong in outline, the cuticle smooth or faintly verruculose: underleaves imbricated, attached in a straight line, obovate to cuneate, averaging 0.7 mm. long, 0.7 mm. broad in the upper part, the margin serrate, the cells as in the leaf: autoiceous (?) or dioicous: female branches short, occurring

singly, with one subfloral innovation, thus appearing lateral, the bracts similar in outline to the leaves, averaging 1.3 mm. long, the ventral margin dentate, the lobule large, 0.85 mm. long, plane, more or less obovate, obscurely bifid, the margins dentate; the bracteole cuneate, similar to the underleaf, 0.9–1.2 mm. long, the margins serrate and coarsely dentate: the perianth mostly 1.5 mm. long, the beak short, the keels densely set with large irregularly tooth laciniae, the dorsal face smooth, the ventral faces each with one or more groups (in one or two rows) of laciniae similar to those of the keels: male branches and sporophytes not seen.

Habitat: On bark of trees in forests.

Distribution: GUIANA: Hb. Hooker, (Y, NY). BRAZIL: Tauau, Spruce (NY). Also in the Indo-Malayan Region.

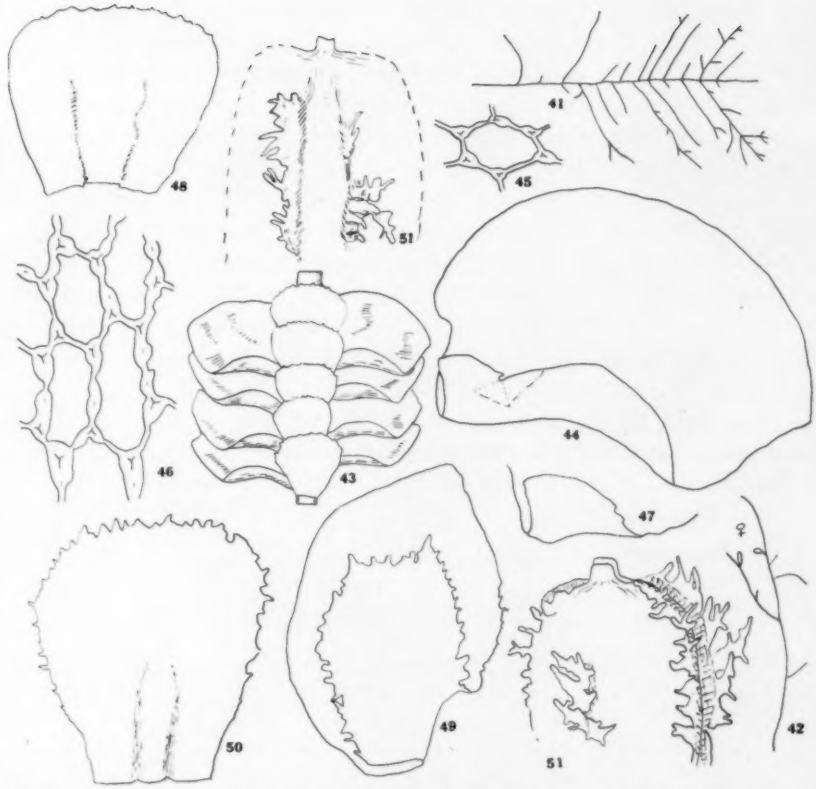
The distinguishing characteristics of the species are its robust habit, dark color, the nearly entire leaves, and small lobules with a short apical tooth; the long-angular cell lumina and conspicuous trigones; the obovate underleaves serrate along the upper margins; and the laciniate wings of the perianth. See figures 41–51.

T. amazonicus and *T. comosus* are very similar in many respects, namely, size of plant, growth habit, and, in a general way, the shape of the leaf and of the leaf cells. The underleaves of *T. comosus*, when well developed, are obovate with a serrate margin (figs. 43, 48), while in *T. amazonicus* (figs. 29, 35), although they are more or less obovate, the apical region is distinctly retuse or more or less 2-toothed. The apical margin is serrate to a greater or lesser degree.

An additional striking distinction is to be found in the parts of the female involucres of the two species. The bracts of *T. amazonicus* are dentate at the apices, and the lobules are long, narrow, and conspicuously bifid with the margins occasionally toothed in the upper part (fig. 36), while those of *T. comosus* are dentate along the ventral margins, and the lobules are long, ovate, obscurely bifid, with the margins coarsely dentate to the base (fig. 49). The bracteoles of *T. amazonicus* are oblong, bifid, and coarsely dentate in the upper part, while those of *T. comosus* are cuneate, and from serrate to dentate throughout. (Compare figs. 37 and 50.) The laciniate wings on the keels of the perianths of *T. comosus* will immediately distinguish that species from *T. amazonicus*, in which the perianth keels are only sparingly dentate (figs. 39–40, 51).

The leaves and underleaves in the vicinity of the female branches and sometimes at the tips of the stems are usually more strongly toothed than elsewhere on the plant. When toothed leaves occur in the region of the female branches they are intermediate in form between ordinary leaves and the bracts and bracteoles.

All the South American material examined was dioicous. Spruce describes the South American material (under *Thysano-Lejeunea dissoptera*)



FIGS. 41–51. *T. cosmos* Lindenb. FIG. 41. Diagram of branching pattern of a sterile stem. FIG. 42. Diagram of branching pattern of a female plant. FIG. 43. Portion of a plant, ventral view, ×15. FIG. 44. A leaf, ×30. FIG. 45. A cell from the apical portion of a leaf, ×400. FIG. 46. Cells from the basal portion of a leaf, ×300. FIG. 47. Lobule, ×30. FIG. 48. Underleaf, ×30. FIG. 49. Female bract, ×15. FIG. 50. Female bracteole, ×30. FIG. 51. Ventral faces of a perianth, ×30. Drawn from the original collection from Guiana.

as "dioica (?)"; Stephani[11] describes both *T. dissopterus* and *T. comosus* as "dioicous," while Verdoorn's description[12] states that the species is "usually monoicous." The portion of the type material from Paulo-Penang which I examined had many well developed perianths but I could find no male branches.

There has been some difference of opinion as to whether the South American plants were actually *T. comosus*, a species widespread in Indo-Malaya. Lindenberg in the original description cited plants in "Paulo Penang, ubi legit cel. Wallich," also "in Guiana lectam accepi ab illustr. Hooker." Spruce[13] considered this interpretation to be incorrect and separated the

[11] Spec. Hep. **4**: 784, 787. 1912.

[12] Verdoorn, op. cit. p. 176.

[13] Trans. Bot. Soc. Edinb. **15**: 107–109. 1885.

South American plants from the "composite species," *T. comosus*, and called the South American plants *Lejeunea* (*Thysano-Lejeunea*) *dissoptera*. He also described the material from Paulo Penang, retaining for it the specific epithet *comosus*. On the other hand, Mitten[14] considered the two to be identical. Stephani's comments[15] concerning the Guiana material are obscure, for he says (discussing *T. comosus*), that only Nos. 85 and 86 represent the true species, moreover the American No. 84 is very similar. Verdoorn[16] has followed Lindenberg in considering the South American and the Asiatic material identical. In my observations of a portion of the type material from both Guiana and Paulo-Penang in the Mitten collection I have not been able to discover any variations of sufficient degree and uniformity by which the two could be separated. The two seem to be identical. Except for the original material from Guiana, I have seen only one other collection from South America, one made by Spruce at Tauau, Brazil. Spruce makes no mention of this collection in his "Hepaticae of the Amazon and Andes."

DEPARTMENT OF BOTANY,
UNIVERSITY OF CINCINNATI.

[14] Hepaticae Indiae Orientalis. Jour. Linn. Soc. Bot. **5**: 89–128.
[15] Die Gattung *Lejeunea* im Herbarium Lindenberg. Hedwigia **29**: 1–23, 1890.
[16] Verdoorn, op. cit. 175.

NEW RUSTS FROM AMERICA AND AFRICA[1]

GEORGE B. CUMMINS[2]

(WITH SEVEN FIGURES)

Puccinia makenensis Cummins, sp. nov. (Fig. 3.) Pycniis non visis. Aeciis hypophyllis, in maculis flavidis non vel leniter incrassatulis 1–5 mm. diam. aggregatis vel plus minusve sparsis, cupulatis, 0.2–0.25 mm. diam.; cellulis peridii angulariter globoideis vel ellipsoideis vel polyhedricis, 14–20 × 16–26 μ, pariete interiore verrucoso 3–3.5 μ cr., exteriore striato 4–5 μ cr.; aeciosporae globoideae vel ellipsoideae, 13–17 × 17–20 μ; membrana hyalina, 0.5–1.0 μ cr., minuteque verruculosa. Urediis nullis. Teliis amphigenis vel plerumque epiphyllis, irregulariter aggregatis, rotundatis vel elongatis, usque ad 1.5 mm. longis, atro-brunneis, subepidermalibus, plus minusve indehiscentibus, loculatis, paraphysibus brunneis coalitis numerosis; teliosporae variabiles sed plerumque clavatae, ad apicem rotundatae, attenuatae vel obtusae, deorsum attenuatae, medio leniter constrictae, 19–27 × (40–)48–66(–75) μ; membrana 1.5–2.5 μ cr., ad apicem 3–8 μ cr., castaneo-brunnea, levi; pedicello persistenti, sporam aequante, flavido.

On *Blepharis boerhaaviaefolia* (*maderaspatensis*), Makene, Sierra Leone, Jan. 28, 1939, *F. C. Deighton 1741.* TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

The aecia and teliospores are similar to those described for *Puccinia blepharidis* P. Henn., although the teliospores are somewhat longer, but the loculate, paraphysate telia of *P. makenensis* are distinctive. It is probable that *Aecidium blepharidis* Pat. & Har., which occurs on the same host, is synonymous with *P. makenensis.*

Puccinia multiloculata Cummins, sp. nov. (Fig. 1.) Pycnia epiphylla, subepidermalia, globosa, 100–150 μ diam.; perpauca vel frequenter non visa. Aecia hypophylla, subepidermalia, dense aggregata in maculis 1–2 mm. diam., breviter cupulata, 0.15–0.25 mm. diam.; cellulis peridii rhomboideis vel oblongo-ellipsoideis, 14–20 × 23–30 μ, pariete interiore verrucoso 2.5–3 μ cr., exteriore striato 4–5 μ cr.; aeciosporae globoideae, 13–16 × 15–18 μ; membrana hyalina, 0.5 μ cr., sublevi. Uredia ignota, verissimiliter nulla. Telia petiolicola, elongata, usque ad 7 mm. longa, atra, subepidermalia, indehiscentibus, loculata, paraphysibus numerosis brunneis coalitis; teliosporae (rarius 2-septatae) clavatae vel cylindraceae, ad apicem rotundatae, truncatae vel attenuatae, ad basim attenuatae, medio leniter constrictae, 13–19 × 36–62 μ; membrana pallide castaneo- vel aureo-brunnea, 1.5 μ cr., ad apicem 3–6 μ cr., levi; pedicello persistenti, sporam aequante, intense brunneolo.

On *Thunbergia cynanchifolia*, Segbwema, Sierra Leone, Dec. 11, 1937,

[1] Contribution from the Department of Botany, Purdue University Agricultural Experiment Station, Lafayette, Indiana.

[2] I am indebted to Dr. G. R. Bisby, Imperial Mycological Institute, Kew, England, Mr. H. E. Parks, Trinidad, Calif., and Dr. John A. Stevenson, Bureau of Plant Industry, Washington, D. C., who made available for study certain of the specimens reported here.

F. C. Deighton 1460. TYPE in the Arthur Herbarium and the Herbarium of the Imperial Mycological Institute.

This species is distinct from other species of *Puccinia* on *Thunbergia* because of the loculate, paraphysate telia. The pedicel of the teliospores is usually darker than the base of the spore. It is doubtful, judging from descriptions, if the aecia are distinguishable from those of *P. thunbergiae* Cooke and *P. tandaaiensis* Hopkins. Only one telial group was seen but the telia are probably not always confined to the petioles.

Puccinia paroselae Cummins, sp. nov. (Fig. 2.) Urediis hypophyllis vel caulicolis, subepidermalibus, sparsis, rotundatis vel oblongis, 0.4–1.2 mm. longis, cinnamomeis; urediosporae obovoideae, ellipsoideae vel late ellipsoideae, 15–20 × 20–29 (–33) μ; membrana 1.5 μ cr., cinnamomea, minuteque echinulata, poris germ. 3 vel 4, aequatorialibus vel plus minusve sparsis. Teliosporae in uredia ellipsoideae vel oblongo-ellipsoideae, utrinque ro-

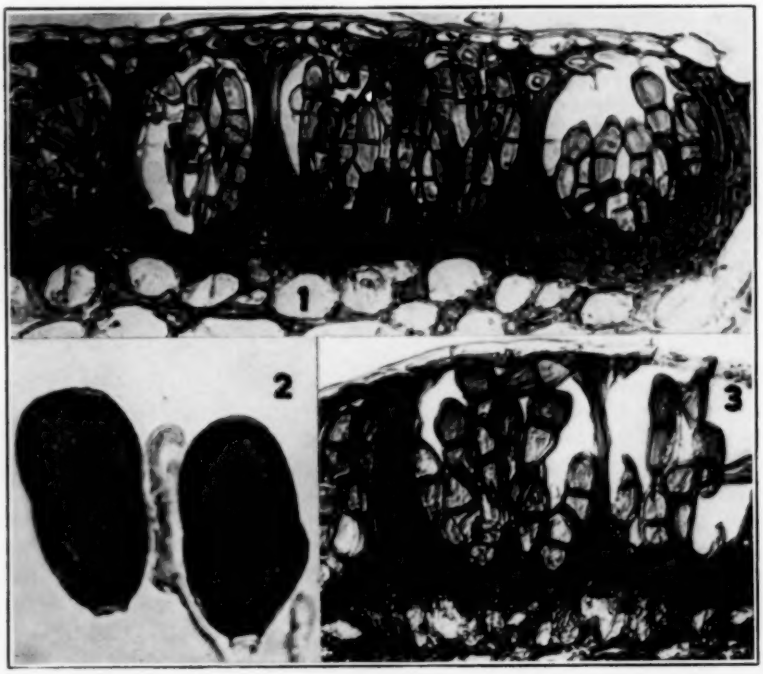


FIG. 1. Photograph of a free-hand, unstained section of the loculate telium of *Puccinia multiloculata*, showing the abundant development of the brown paraphyses and the concolorous, subjacent, stroma-like tissue. × 240.

FIG. 2. Two teliospores of *Puccinia paroselae;* note that the pore of the upper cell is approximately apical while that of the lower cell is near the short, fragile pedicel. × 800.

FIG. 3. Photograph of a free-hand, unstained section of the telium of *Puccinia makenensis*, showing the brown paraphyses which divide the sorus into locules. × 240.

tundatae vel ad basim leniter attenuatae, medio leniter constrictae, 21–25 × 35–42(–45) μ; membrana 2–2.5 μ cr., pallide castaneo- vel aureo-brunnea, minuteque verrucosa; poro superiore apicali vel subapicali, inferiore infra medium loculum sito; pedicello hyalino, fragili, brevissimo.

On *Parosela mollis*, roadside in Santa Rosa Canyon, Riverside Co., Calif., Feb., 1940, *H. E. Parks & Marvin Jordan 6430.* TYPE in the Arthur Herbarium.

According to the relationship of the host one would expect this rust to belong in the genus *Uropyxis* but the presence of only a single germ pore in each cell of the teliospore excludes it from that genus.

Puccinia puritanica Cummins, sp. nov. (Fig. 4.) Urediis hypophyllis, subepidermalibus, sparsis, rotundatis vel oblongis, 0.3–0.8 mm. longis, pallide cinnamomeis; urediosporae late ellipsoideae, ellipsoideae vel obovoideae, 16–20 × 20–25 μ; membrana 1.5 μ cr., pallide cinnamomea, minuteque echinulata; poris germ. 2, superaequatorialibus. Teliis conformibus; teliosporae clavatae vel oblongae, ad apicem rotundatae, deorsum attenuatae, medio constrictae, 12–17 × 25–37(–40) μ; membrana 1–1.5 μ cr., ad apicem 4–8 μ, flavida vel pallide aureo-brunnea, levi; pedicello hyalino, sporam subaequante vel breviori. Statim germ.

On *Carex pennsylvanica,* Waltham, Mass., Oct. 1, 1910, *A. B. Seymour 10.* TYPE in the Arthur Herbarium and in the Mycological Collections of the Bureau of Plant Industry, U. S. Department of Agriculture.

The urediospores of this rust are indistinguishable from those of *Puccinia extensicola* Plowr. or of *Uromyces perigynius* Halst. Telia of the latter species are also present in this specimen and, while some of the uredia may belong with them, sectioning proved that the nearly colorless teliospores of *P. puritanica* occur in the uredia as well as in separate sori. The similarity of the uredia of the two species, the close association of the two kinds of telia and the fact that the two-celled teliospores germinate at once lead to the speculation that perhaps a single species was present, with the *Uromyces* spores representing the resting stage. Such a life cycle would be unique but possibly could occur. However, numerous sections of the telia failed to reveal mixture of the one- and two-celled teliospores.

The relationship of *P. puritanica* is uncertain. While the urediospores are like those of *P. extensicola* the teliospores show no similarity but are near those of the Philippine species, *P. constata* Syd.

Uromyces ictericus Cummins, sp. nov. (Fig. 5.) Pycniis ignotis. Aeciis epiphyllis, subepidermalibus, aggregatis in maculis pallidis 2–4 mm. diam., aperidiatis, poro apertis; aeciosporae catenulatae, globoideae, ellipsoideae vel oblongo-ellipsoideae, 16–23 × 20–30 μ; membrana 1–1.5 μ cr., hyalina vel pallide flavida, verrucosa. Urediis nullis. Teliis hypophyllis, subepidermalibus, aggregatis, rotundatis, oblongis vel confluentibus, pulvinatis, cinnamomeis vel flavidis; teliosporae late ellipsoideae, ovoideae vel obovoideae, 15–20 × 20–30 μ; membrana 1.5–2 μ cr., ad apicem 3–5 μ cr., flavidula vel

hyalina, levi; pedicello persistenti, hyalino, sporam aequante vel longiore.

On *Iresine celosia*, Aguas Amargas, Quezaltenango, Gautemala, Jan. 30, 1917, *E. W. D. Holway 803*, TYPE; Solola, Guatemala, Jan. 28, 1915, *Holway 141*. Type in the Arthur Herbarium.

These collections have previously been assigned to *Uromyces iresines* Lagerh., a South American species which has similar aecia but larger (23–30 × 27–40 μ) aeciospores with thicker walls (1.5–2.5 μ) and ovoid, larger teliospores (18–24 × 33–44 (–47) μ). The teliospores are similar to those of *Uromyces clarus* Jacks & Holw., a species possessing uredia with striate urediospores.

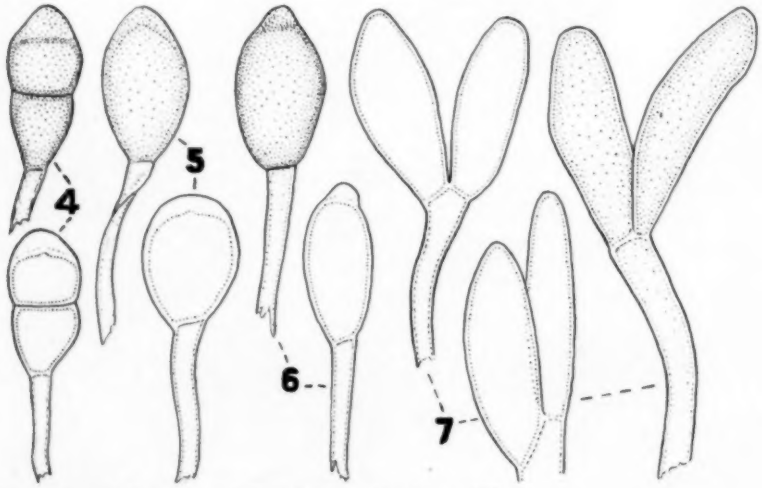


FIG. 4. Two teliospores of *Puccinia puritanica*. × 650.

FIG. 5. Two teliospores of *Uromyces ictericus*, a Guatemalan species previously confused with the South American *U. iresines* Lagerh. × 650.

FIG. 6. Two teliospores of *Uromyces necopinus*, a species previously included in the demicyclic *U. affinis* Wint. × 650.

FIG. 7. Teliospores of *Ypsilospora baphiae*, a rust in which the teliospores are borne in laterally free pairs on a common pedicel. × 650.

Uromyces necopinus Cummins, sp. nov. (Fig. 6.) Urediis incertis; urediosporae obovoideae vel late ellipsoideae, 17–20 × 20–29 μ; membrana cinnamomeo-brunnea, 1.5 μ cr., minuteque echinulata; poris germ. 3, aequatorialibus. Teliis amphigenis, subepidermalibus, sparsis vel plus minusve aggregatis, rotundatis, 0.2–0.5 mm. diam., pulvinatis, cinnamomeis; teliosporae ovoideae, ellipsoideae vel oblongae, 10–18 × 25–36 μ; membrana 1–1.5 μ cr., ad apicem 5–7 μ cr., pallide aureo-brunnea vel flavida, levi; pedicello persistenti, hyalino, sporam aequante vel longiore.

On *Hypoxis hirsuta*, vicinity of Lake Katrine, Ulster Co., N. Y., Aug. 17, 1916, *P. Wilson 402*, TYPE; Norwich, Conn., Aug. 17, 1889, *W. A. Setchell*. Type in the Arthur Herbarium.

Uromyces necopinus has been confused with *U. affinis* Wint. from which

it is readily separable because of its smooth teliospores.

Jackson (Mycologia **18**: 157. 1926) has pointed out that *Uredo hypoxidis* (Bres.) P. Henn. should not be considered as synonymous with *U. affinis*. *U. affinis* was originally described as lacking uredia and there is no present evidence to contradict this. In fact, Demetrio's original collection is the only specimen in the Arthur Herbarium.

Ypsilospora Cummins, gen. nov. (*Pucciniaceae*.) Pycnia subcuticularia, hemispherica vel conoidea. Aecia et uredia nulla vel adhuc ignota. Telia subepidermalia; teliosporae unicellulares inter se liberae, binae in apice pedicello communi natae, hyalinae vel subhyalinae, statim germinantes ad apicem in promycelium typicum elongatae.

TYPE SPECIES: *Ypsilospora baphiae*.

Ypsilospora baphiae Cummins, sp. nov. (Fig. 7.) Pycnia subcuticularia, hemisphaerica vel conica, maculis incrassatulis usque ad 7 mm. diam. occupantibus. Aecia et uredia nulla. Telia subepidermalia, plus minusve profunde immersa, amphigena, inter pycnia sparsa, rotundata, 0.15–0.25 mm. diam. vel confluentibus, flavida; teliosporae cylindraceae vel oblongo-ellipsoideae, 11–15 × 34–50 μ; membrana hyalina, 1 μ cr. vel ad apicem 2 μ cr., levi; pedicello hyalino, persistenti vel fragili, sporae aequante vel breviore.

On *Baphia nitida*, Maboma, Sierra Leone, Nov. 5, 1939, *F. C. Deighton 2138*. TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

This interesting microcyclic rust has 1-celled teliospores borne in pairs at the apex of a common pedicel. The pedicels disjoin from the sorus, the mature spores are pushed upward by the development of younger spores below and accumulate above the sorus. The arrangement of two teliospores upon a common pedicel is similar to that which characterizes the teliospores of *Sphenospora*, except that here the two spores have no common wall. It should be noted that the teliospores of *Sphenospora copaiferae* (P. Henn.) Syd. are described (Monogr. Ured. **4**: 584. 1924) as ". . . am Septum meist ziemlich tief eingeschnürt. . . ." *Copaifera* is likewise a genus of the Leguminosae and the two rusts may prove to be closely related.

Uredo aspiliae-latifoliae Cummins, sp. nov. Uredia hypophylla, subepidermalia, rotundata, 0.2–0.4 mm. diam., pulverulenta, cinnamomea; periphysibus inconspicuis, cylindraceis vel ampullaceis, 8–14 × 30–50 μ, membranis 1 μ cr., ad apicem 1.5–3 μ cr., pallide brunneis; urediosporae ellipsoideae, obovoideae vel globoideae, 17–23 × 19–27 μ; membrana 1.5 μ cr., cinnamomeo-brunnea, moderate echinulata; poris germ. 2, aequatorialibus.

On *Aspilia latifolia*, Kenema, Sierra Leone, Dec. 5, 1937, *F. C. Deighton 1505*. TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

This species differs from previously described rusts on *Aspilia* by the presence of paraphyses in the uredia.

Aecidium brideliae-micranthae Cummins, sp. nov. Pycnia epiphylla, subepidermalia, globosa, 120–150 μ diam., paraphysata. Aecia hypophylla, subepidermalia, dense aggregata in maculis atro-brunneis usque ad 15 mm. diam., flavida, breviter cupulata, 0.15–0.2 mm. diam.; cellulis peridii fragilis, plus minusve isodiametricis, 15–20 μ diam., minuteque verruculosis; aeciosporae globoideae, 10–15 μ diam.; membrana 0.5 μ cr., hyalina, minuteque verruculosa.

On *Bridelia micrantha*, Ngelehun, Sierra Leone, Apr. 19, 1940, *F. C. Deighton 2269*. TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

Aecidium cynanchi Cummins, sp. nov. Pycniis epiphyllis, globosis, 80–110 μ diam., subepidermalibus, paucis. Aeciis hypophyllis, laxe aggregatis in maculis pallidis usque ad 12 mm. diam., cupulatis, margine revoluto; cellulis peridii angulariter globoso vel oblongo, 14–20 × 19–25 μ; pariete interiore verrucoso 3 μ cr., exteriore levi 2 μ; aeciosporae globoideae vel ellipsoideae, 12–17 × 14–18 μ; membrana 1 μ cr. hyalina, minuteque verruculosa.

On *Cynanchum manni*, Nganyahun, Sierra Leone, Apr. 19, 1940, *F. C. Deighton 2270*. TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

Aecidium leonense Cummins, sp. nov. Pycnia non visa. Aecia caulicola, ubique aequaliter denseque distributa, totam superficiem occupantia, subepidermalia, breviter cupulata, 0.2–0.3 mm. diam.; cellulis peridii plus minusve laxe conjunctis, rhomboideis, 13–16 × 15–19 μ, pariete interiore moderate verrucoso 3 μ cr., exteriore 3–3.5 μ cr. levi; aeciosporae globoideae vel oblato-sphaeroideae, 11–16 × 11–15 μ; membrana hyalina, 1 μ cr., minuteque verruculosa.

On *Dioscorea* sp., Sembehun, Sierra Leone, Apr. 26, 1940, *F. C. Deighton 2282*. TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

Notes by the collector of this systemic rust are as follows: "Causing a witch-broom with thickening of the attacked stems. From appearance, very possibly a perennial rust."

THE ARTHUR HERBARIUM,
PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION.

STUDIES IN THE FAMILY WORONINACEAE—I. DISCUSSION OF A NEW SPECIES INCLUDING A CONSIDERATION OF THE GENERA PSEUDOLPIDIUM AND OLPIDIOPSIS

D. A. McLarty

(WITH TWENTY-SIX FIGURES)

INTRODUCTION

The genus *Olpidiopsis* was established by Cornu in 1872 to include five species which he found parasitizing various members of the Saprolegniales. For three of these species Cornu described thick-walled resting spores with one or several attached empty cells which he assumed were antheridia. Although he did not mention it specifically as a generic character, this "cellule adjacente," which Cornu observed in only three of his five species, came to be regarded as the distinguishing character of the genus. In 1878 Reinsch observed the passage of the contents of the smaller into the larger thallus, and since that time the resting spores of *Olpidiopsis* have been generally considered to arise as the result of definite sexual fusions.

A few years later, however, Fischer (1880) failed to observe antheridial cells in what he considered to be *O. Saprolegniae*. Accordingly in 1882 he rejected the "adjacent cell" character as diagnostic for the genus and restricted *Olpidiopsis* to species which produce asexual resting spores. Subsequent studies, however, convinced Fischer that his earlier observations had been incorrect, and in 1892 he restored the genus to its original status and established a second genus, *Pseudolpidium*, to include *Olpidiopsis*-like species with asexual resting spores. In his genus Fischer included *P. Saprolegniae* and *P. fusiforme*, for which he described resting spores, and four additional very dubious species for which no resting spores were observed.

Since the time of Fischer no critical work has been done on the species which he observed but many new species of *Olpidiopsis* and *Pseudolpidium* have been described, and generic distinctions have been made solely upon the basis of the presence or absence of antheridial cells attached to the resting spores. Species of these two genera have repeatedly been reported as occurring simultaneously in the cells of various hosts, although there is no record of the individual species, in such cases, having been isolated in pure cultures. In swollen filaments of *Achlya flagellata* which appeared to be infected with several species, the author (1939) immediately recognized *P. Saprolegniae* and *P. fusiforme*. In addition spherical, thick-walled resting spores, similar to the type described by Butler (1907) for certain *Pseudolpidium* species, were observed with occasional *Olpidiopsis* resting spores. It was found at once, however, that the spiny bodies which Fischer described

as resting spores are nothing more than thin-walled zoosporangia which liberate zoospores directly without becoming dormant. It was thus obvious that Fischer's genus *Pseudolpidium*, based on the misinterpretation of these sporangia, is no longer valid. This viewpoint has been confirmed by the subsequent discovery of similar spiny sporangia in *O. vexans*, *O. fusiformis*, *O. varians*, and *O. Saprolegniae* by Shanor (1939).

When monospore cultures were established, the author (1939) found, however, that he was not dealing with several organisms but with a single species which produces smooth and spiny zoosporangia and forms thick-walled resting spores with or without attached antheridial cells. This discovery immediately raised the question whether or not any generic distinction can be made on the basis of this character of the resting spore. Pending further investigation of the nature of sex in this group, however, the author (1939) suggested that the genus *Pseudolpidium*, amended in accordance with the new facts, might be maintained for the asexual species described by Butler (1907), and that the organism with which we are dealing might be regarded tentatively as a *Pseudolpidium* species which, although predominantly asexual, may display some sexuality.

Since that time a thorough investigation of the variations in structure and sexual expression displayed by this new species has been made in an effort to establish its proper relationships and to evaluate some of the characters upon which generic and specific distinctions have been made in the past. Some of the results of this study are recorded in this paper.

MATERIALS AND METHODS

The technic employed in securing and maintaining the parasite is an adaptation of the method reported by Miss Berdan (1939). A pure stock culture of *Achlya flagellata* was maintained on Difco potato dextrose agar, while the parasitized host cultures were grown on sterile hemp seeds in sterile charcoal water. Transfer and renewal cultures were prepared by placing an infected "seed culture" in fresh charcoal water with a fresh *Achlya* culture. By repeated washing of the "seed culture" with sterile distilled water from a pressure wash bottle, protozoa were eliminated, and bacterial contamination was reduced to a minimum. It was found convenient to hold the culture in the depression of a moist chamber slide and to use a small aquarium pump to develop pressure sufficient to thoroughly clean the culture. Temperatures higher than approximately 25° C. were unfavorable, since they induced dormancy of the sporangia. This dormancy, however, could be broken by subjecting the culture to a temperature of about 15° C. for 24 hours.

Monosporangial cultures were prepared by collecting a few zoospores in a micropipette as they emerged from the sporangium and placing them

in sterile charcoal water containing a pure culture of *Achlya* growing on a small block of agar. After a period of 24 hours, isolated sporangia appeared in the *Achlya* filaments, and with the aid of a low power dissecting microscope the parasitized filaments were separated without disturbing the sporangia. Filaments with single sporangia were then transferred to a culture dish containing pure *Achlya*, and in this way monosporangial infections were secured.

Similarly monospore cultures were obtained by collecting with a micropipette a drop of water containing several zoospores. The water was then spaced out in tiny droplets on a glass slide, and those containing a single zoospore were picked up again in sterile micropipettes and added to pure *Achlya* cultures.

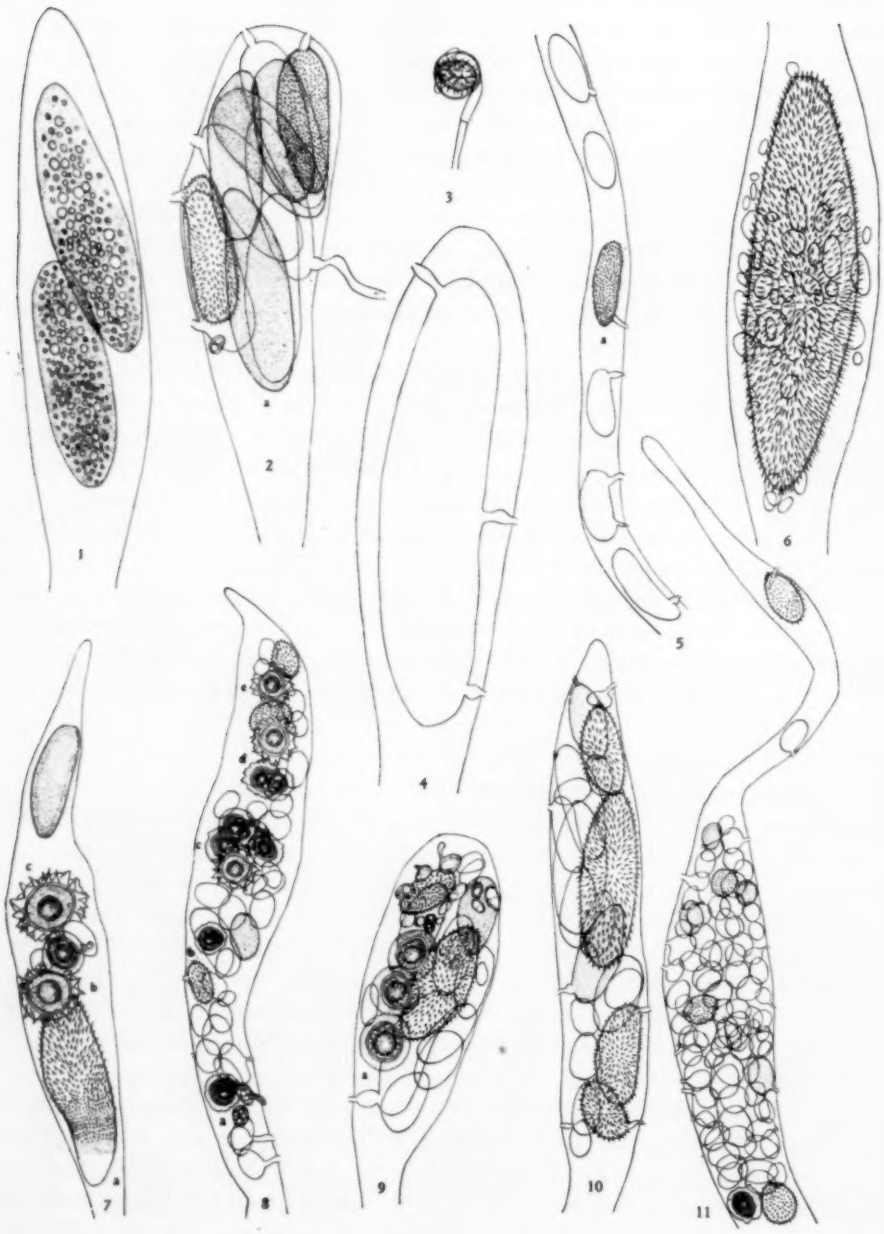
The infection and subsequent progressive stages in the development of the sporangia and resting spores of the parasite were observed in hanging drop cultures. When a small culture of *Achlya*, which had been allowed to remain for a few moments in water containing numerous zoospores, was lifted in a large pipette and placed on a cover-slip, the filaments spread out and clung close to the surface in a thin film of water, thus making it possible to use the oil immersion lens for observations. For the study of the developing zoosporangia, agar block cultures were used, because where the host presumably has a limited supply of food the thalli develop and mature rapidly without the interjection of long rest periods. For the study of resting spore development, the host was grown on fragments of raw meat.

OBSERVATIONS

Variations in Size, Shape, and Echinulation of the Zoosporangia. All monospore infections of *Achlya* so far observed have always resulted in the formation within the host filament of large, solitary, thin-walled zoosporangia (fig. 4). At maturity such solitary sporangia liberate large numbers of zoospores which re-infect the tips of young *Achlya* filaments. From such a secondary, multiple infection all the types of sporangia illustrated in figures 1–11 may result.

Correlations between the size of the sporangia, the size of the localized swellings of the host hyphae, and the number of sporangia in each swelling were sought. In this connection, however, we are dealing with large, aseptate filaments in which it is difficult to determine the unit of host protoplasm involved. The vigor of the host filaments and the volume of protoplasm which they might contain, moreover, vary so greatly that the interpretation of sporangial variation in terms of population counts and measurements proved impractical. It was soon found better to rely upon observational methods.

In hanging drop cultures it was possible to determine the approximate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numbers of zoospores infecting various filaments and to determine also the time at which certain infections took place relative to other local infections. As described above, solitary infections give rise to solitary sporangia which may become very large (fig. 4) if the host filament contains copious amounts of protoplasm but which will mature quickly without attaining great size if the supply of host protoplasm is limited. When two or several zoospores penetrated a filament more or less simultaneously, smaller sporangia of somewhat uniform size developed (figs. 1, 2). The size of the sporangia decreases as the number in the filament increases.

In not too congested filaments the sporangia attain appreciable size and assume a more or less ellipsoidal shape. When filaments were beset by large numbers of spores, however, large swellings, filled with small, spherical or oval sporangia measuring 11.5–50 microns in their largest diameter, were formed (fig. 11). It was also observed that when multiple infection of a filament which already contained one or several developing thalli occurred, the numerous sporangia formed were dwarfed (fig. 6). Apparently in such cases the older thalli absorb the bulk of the food and consequently deprive the younger thalli of adequate nourishment.

The ornamentation of the walls of zoosporangia varies from very fine echinulations (fig. 2a) to large heavy bristles (fig. 6). Attempts were made to correlate the production of bristles with the age of the culture, the vigor of the host, and other general environmental factors. No such correlations could be established, however, since it was found that smooth and rough-walled sporangia were produced simultaneously side by side (figs. 2, 10), and the entire range of variation from smooth to extremely rough walls was often observed on a single sporangium (fig. 7a).

The progressive stages of bristle formation were often observed in hang-

Explanation of figures 1–11

FIG. 1. Two elongate thalli of *O. Achlyae* in a swollen tip of an *Achlya* filament. ×93. FIG. 2. Several smooth and rough-walled empty zoosporangia of approximately equal size in a swollen filament. ×93. FIG. 3. A small, spiny zoosporangium in an *Achlya* oogonial cell. ×93. FIG. 4. A large solitary zoosporangium, with three exit tubes, in a swollen *Achlya* filament. ×93. FIG. 5. Several small, empty, smooth and rough-walled zoosporangia which have matured in a filament without causing any appreciable swelling of the host cell. ×93. FIG. 6. A single large, spiny zoosporangium in a swollen filament with numerous smaller, smooth sporangia. ×93. FIG. 7. A swollen *Achlya* filament containing a parthenogenetic resting spore of *O. Achlyae*, two sexual resting spores *b* and *c* and two rough-walled sporangia; sporangium *a* is smooth at one end and heavily bristled at the other. ×93. FIG. 8. A swollen *Achlya* filament with numerous, small, smooth and rough-walled zoosporangia and asexual (*a–d*) and sexual (*e*) resting spores. ×93. FIG. 9. Large and small, smooth and rough-walled zoosporangia with three smooth-walled resting spores (*a*). ×93. FIG. 10. Oval to elongate, smooth and rough-walled zoosporangia in a slightly swollen filament. ×93. FIG. 11. Numerous spherical to oval, smooth and rough-walled zoosporangia in a swollen *Achlya* filament; two isolated thalli have caused little swelling of the host filament in their vicinity. ×93.

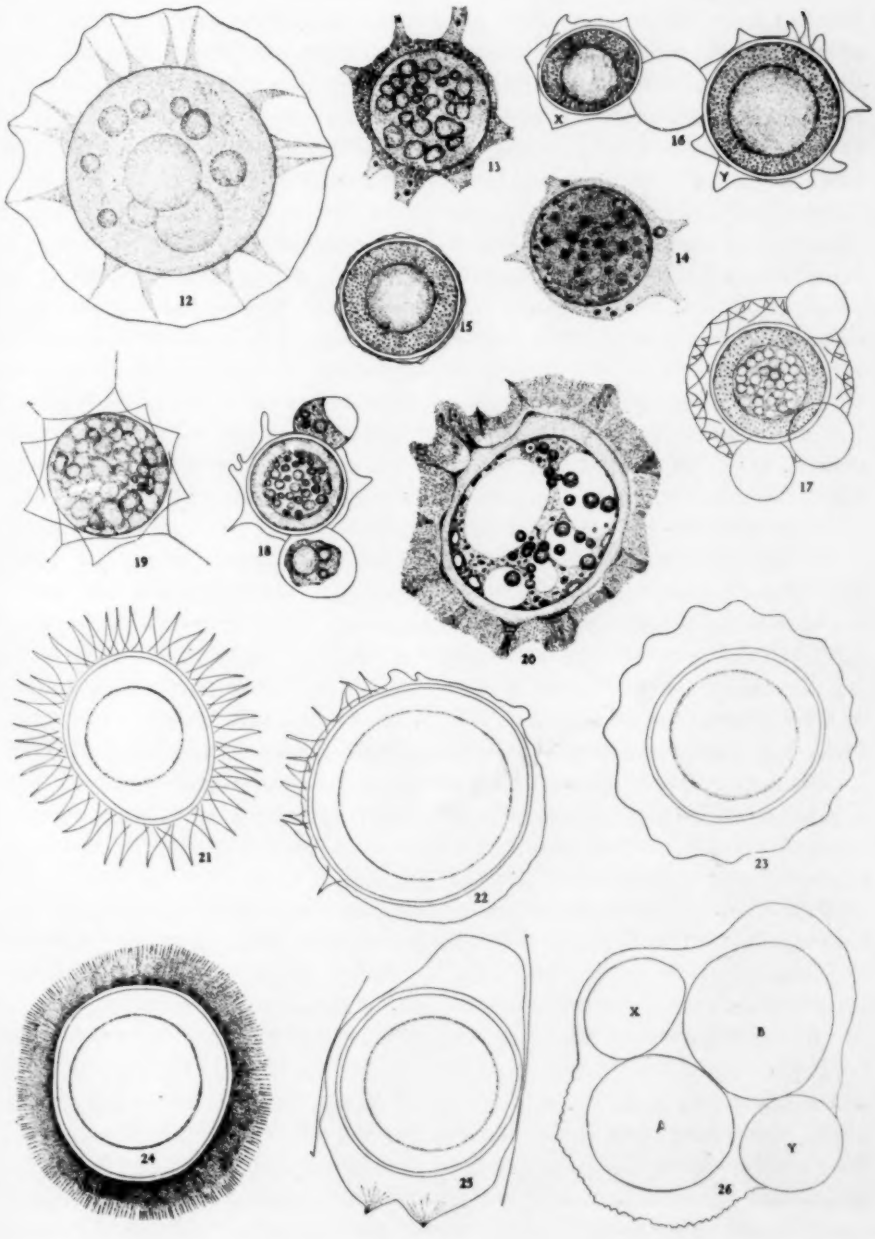
ing drop cultures. On the surface of sporangia which had attained approximately their mature size but were still surrounded by an appreciable amount of visible host protoplasm, small, hyaline, indefinite bristles were sometimes discernible. Such bristles increase in number, size, and density until, at maturity, the sporangium may appear similar to that shown in figure 6. As this development takes place the visible host protoplasm gradually diminishes until, at maturity, the sporangium is suspended in a hyaline medium. Although it has not been conclusively demonstrated that these bristles arise by a localized deposition of host protoplasm, this is suggested by the fact that they develop as the refractive material about them diminishes. This is in agreement with the observations of Fischer (1882). Furthermore, when such rough-walled sporangia are treated with zinc chloro-iodide, the wall stains blue, but the bristles give no cellulose reaction. The actual chemical nature of the bristles, however, remains unknown.

These observations on living zoosporongia seem to indicate that variations in their size are dependent upon the vigor of the host, the number of thalli developing in a given locality, and, within a single filament, the time of penetration relative to other local infections. They vary, accordingly, from large, solitary, cylindrical sporangia to small, spherical ones which develop in congested filaments. Although the factors controlling the formation of bristles are obscure, they appear to arise by a direct, localized deposition of host protoplasm upon the surface of the thalli.

Development and Variations of the Exospore. The great variability which characterizes the exospore, in this species is of particular interest in view of the great stress which has been placed upon this structure in the determination of species of *Pseudolpidium* and *Olpidiopsis.*

Explanation of figures 12–26

FIG. 12. Origin of spines of the exospore within the hyaline layer drawn from living material. ×580. FIGS. 13–15. Successive stages in the development of a thin, warty exospore on a resting spore which absorbed most of the host protoplasm during its early developmental stages. ×470. FIG. 16. An empty male cell attached to two mature resting spores. ×470. FIG. 17. A mature sexual resting spore with three empty male cells attached; margin of the homogeneous layer is visible about the apices of the spines. ×470. FIG. 18. A mature resting spore with two attached male cells which still contain their contents. ×470. FIG. 19. Cytoplasmic strands running from the apices of the broad-based spines of an asexual resting spore. ×470. FIG. 20. A developing resting spore stained with haematoxylin showing origin of spines within the homogeneous layer by centripetal condensation of protoplasm along definite lines. ×580. FIG. 21. A parthenogenetic resting spore bearing long, narrow spines. ×580. FIG. 22. A mature resting spore with an exospore which is part smooth and part spiny. ×580. FIG. 23. A mature asexual resting spore of *O. Achlyae* possessing an undulant exospore. ×580. FIG. 24. A mature resting spore bearing a halo of hair-like spines. ×580. FIG. 25. A mature resting spore of *O. Achlyae* illustrating how the development of the exospore has conformed with the wall of the host filament—i.e., with the distribution of the host protoplasm. ×580. FIG. 26. Two sexual resting spores *A* and *B* with their associated male cells *X* and *Y* which have been enveloped by a common wall. ×580.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Young developing resting spores in the living condition can be distinguished from incipient zoosporangial thalli at a fairly early stage by their more opaque protoplasmic content and, to some extent, by the noticeably thicker layer of granular, degenerating host protoplasm which usually surrounds the young resting spores. The exospore usually first becomes evident as a homogeneous, amorphous layer which develops centripetally around the thallus, gradually replacing entirely the mass of granular host protoplasm. At maturity, this layer may maintain a fairly even contour (fig. 23), although, in stained preparations, radially arranged lines, which appear to be regions of condensation, may be observed extending inward from the outer margin of the exospore. In most cases, however, this homogeneous layer becomes organized, to a greater or lesser degree, into spines of various sorts (figs. 17, 21, 22, 24). Such spines, the beginnings of which can often be observed in living material as slightly more opaque, conical regions (fig. 12), are elaborated within the confines of the homogeneous layer, the outer margin of which often remains visible for some time (fig. 17). A resting spore, fixed and stained in a stage of development comparable to that shown in figure 12, is illustrated in figure 20. A tendency for the lines of deposition to become somewhat localized and organized into conical "bundles," which seem to represent incipient spines, is striking. It is to be further noted that the lines of deposition do not extend all the way in but appear to be developing from the outer margin of the layer toward the centre. This observation is in agreement with that of Butler (1907) on *Pseudolpidium Pythii*, for which he describes the spines of the resting spores as arising within a light band "by condensation of protoplasm along definite lines" centripetally.

On a few spores spines have been seen to arise apparently by direct deposition of host protoplasm without the formation of a homogeneous layer. Cytoplasmic strands were usually observed to radiate from the tips of such spines as were newly formed (fig. 19).

Like the bristles of the zoosporangia, the exospores fail to react with zinc chloro-iodide, in contrast to the endospore which gives a brilliant cellulose test. Attempts to demonstrate the actual chemical composition of the exospore have been unsuccessful. It can be definitely said, however, that its deposition is intimately associated with the layer of host protoplasm directly impinging upon the thallus. Figure 25 illustrates a spore the formation of whose exospore has apparently been governed by the limitations of the wall of the host filament—i. e., by the distribution of the host protoplasm. The homogeneous layer seems to result from a direct deposition of host protoplasm, and the organization of spines seems to be accomplished by a regional condensation and deposition of this substance along more or less radial lines.

Strong evidence in support of this interpretation is the very poor development of exospores by resting spore thalli which use up most of the host

protoplasm in their early developmental stages (figs. 13–15). Such spores, at maturity, may be enclosed by a very thin, warty exospore; the outer wall of some that were observed was almost entirely lacking. It might be argued that the host protoplasm is first absorbed by the thallus and later the exospore is secreted. In this case, accordingly, it would be assumed that most of the food material was needed by the maturing thallus and that little excess was left available for wall secretion. The deposition of the exospore begins fairly early, however, and despite its increasing thickness the host protoplasm steadily diminishes. The homogeneous layer might be confused, in certain respects, with the digestion cavity which often surrounds intracellular parasites. Incipient resting spores which have been dissected out at this stage, however, have been found to be enclosed in a definite, structural layer which does not appear to be a region of digestion or absorption. Judging from the difficulties encountered in bringing about penetration of mature spores by fixatives and intra-vitam stains, it seems improbable that much absorption by the thallus would go on after the formation of the exospore has begun. Consequently, the gradual disappearance of the host protoplasm which takes place as the exospore layer increases in thickness is best explained by assuming direct deposition of host protoplasm upon the surface of the thallus. Figure 26, drawn from sectioned and stained material, shows two resting spores A and B, with their related male cells, X and Y respectively. It is to be noted that their exospores are completely confluent and that male cell X is entirely surrounded and embedded. Such a condition seems to suggest exospore production by deposition and direct transformation of host protoplasm rather than separate secretion by each individual thallus.

A consideration of the various configurations which the exospores of mature resting spores of this species may assume is interesting and suggestive of the synonymy which might arise by attributing false significance to these variations. Mature resting spores of our species are often invested by a dense layer of broad based spines similar to those described for *O. fusiformis* and *O. minor* (fig. 17). Sawada (Tokunaga 1933) in 1912 described a species, *P. stellatum*, solely upon the basis of the resting spores observed. These spores, which he describes as similar to those of *O. minor* but lacking attached male cells, are simulated by asexual spores of our species. Long, tapering spines (fig. 21) similar to those described for *O. Saprolegniae* have also been observed, while undulating exospores like those described for *O. major* and *P. incrassata* are not uncommon in cultures of the species here considered (fig. 23). Spores surrounded by a halo of hair-like spines or fibrillae simulating the spores described by De Wildeman (1895) for *O. fibrillosa* regularly occur (fig. 24), while resting spores which have developed under conditions providing a minimum of nourishment often possess,

at maturity, a thin, warty exospore similar to that described by Barrett (1912) for *O. vexans* (fig. 15). In addition, many other irregular variations of the exospore are commonly encountered in cultures of this species (figs. 16, 18, 22, 25).

It is not maintained that all the species whose resting spores are simulated by this one extremely variable organism are necessarily invalid. Nevertheless, the apparent method of formation of the exospore and the infinite variation which it may exhibit within one species indicate that it is not an infallible diagnostic character upon which to base generic distinctions. When all species concerned have been re-collected and critically studied in pure culture, we may learn that many of them are synonymous while others, which may be confined to various definite hosts, may prove to be physiological strains of a few distinct species.

Sex Determination. When Cornu (1872) observed small, empty thalli attached to larger resting spore thalli he assumed that the smaller cells were antheridia. His belief was confirmed in 1878 when Reinsch observed the movement of the contents of the smaller into the larger thallus. Since that time this interpretation has been generally accepted and the terms "antheridium" and "oogonium" have been applied to the smaller and larger thalli, respectively, and the fusion of these cells has been referred to as being a primitive type of oomycetous reproduction. Scherrfel (1925) looks upon the resting spores of *Olpidiopsis* as oospores without periplasm and, upon this basis, he outlines a possible origin of the *Pythium*-Peronosporaceae group from simpler species through *Olpidiopsis*. No investigation of sex determination in these species has ever been attempted, however, and the actual origins of the so-called antheridial and oogonial thalli remain obscure. Barrett (1912) states that when these thalli first become recognizable it is impossible to say whether they have had separate origins or whether they have been derived by an unequal division of a single thallus. He believes, none the less, with all other investigators of *Olpidiopsis* species, that resting spore formation invariably involves fusions of cells. The spores of the species under consideration, however, may be formed with or without fusions while the ratio of so-called sexual to asexual spores may show noticeable variation.

From a series of counts made on resting spores of various culture generations, it was found that only one quarter of the resting spores of our species have attached antheridial cells. It has been noted, however, that the ratio of sexual to asexual spores in consecutive culture generations may show variation which cannot be correlated with any easily recognizable environmental factor. When studying pure cultures of this species it is not unusual to find certain cultures which exhibit no sexuality whatever, while others, growing under the same conditions, display only resting spores of the *Olpidiopsis* type. It has been observed by Barrett (1912), the author,

and others that resting spores are more abundant in cultures grown in stale water, while Diehl (1935) points out that low temperatures have a similar effect. Observations on this species, moreover, have shown that lower temperatures not only stimulate resting spore formation but, in cultures maintained at low temperatures, although the sexual-asexual ratio may still vary, the percentage of sexual resting spores is usually markedly higher.

In several cases, similar to that illustrated in figure 16, male cells attached to two female thalli have been observed. In the thalli illustrated the contents of the male cell passed into the smaller of the two female thalli although the larger thallus matured quite as readily as did the smaller "fertilized" thallus. The passage of only a part of the contents of the male cells into the larger thalli in the "fertilization" process has often been observed, while the total failure of attached male cells to function frequently occurs (fig. 18). It is evident that fusion is not essential to resting spore formation and that male cells, even when present, do not always participate in the maturation of the female thallus.

It has been mentioned by Shanor (1939) that, during his investigation of *O. luxurians*, spores were observed which appeared to be formed asexually, but upon closer observation these proved to be merely "inadvantageously orientated" sexual spores, the male cells of which were hidden from view. That this is not true of the "parthenogenetic" resting spores of our species has been repeatedly shown by dissecting the spores out in glycerine where they could be rolled over and over for examination from all sides.

At the outset it was postulated that the production of sexual and asexual spores by this extremely variable species might be explained on the basis of heterothallism. It was found by the author (1939), however, that heterothallism does not exist in this species, inasmuch as sexual spores occur in cultures which have been propagated from a single zoospore. Moreover, if we are to assume genotypic differentiation of sex in this species, there are basic assumptions to be made which, in themselves, seem to totally discredit any claim of sex segregation. In the case of monospore cultures exhibiting sexuality it would be necessary to assume that the single zoospore from which the culture was propagated was diploid with factors for maleness and femaleness. In the maturation of the primary sporangium formed by the single spore we must further assume that zoospores similar to the original were formed by mitosis, while in other parts of the same sporangium meiosis occurred in the production of genotypically differentiated male and female gametes. These in turn would give rise to the zoosporangial "antheridial" and "oogonial" thalli which appear in the secondary infection. In all the prepared, zoosporangial material studied to date, however, no indication of meiosis has been found to support this assumption which, in itself, seems improbable enough to discredit the entire hypothesis.

It has been stated above that low temperatures appear to increase the percentage of sexually formed resting spores, while the ratio of sexual to asexual resting spores varies constantly without any apparent relation to environmental factors. As will be more clearly brought out in a following paper, the male and female thalli of this species have been found to be multinucleate and essentially similar to the zoosporangial thalli. The mature resting spores are likewise multinucleate, and upon germination they function as sporangia, liberating zoospores through an exit tube. In this regard these resting spores differ from the uninucleate resting spores which Hillegas (1940) has observed for *Endochytrium operculatum*, which germinate indirectly by producing an evanescent zoosporangium in which nuclear divisions take place prior to the delimitation of zoospores. It seems, at least in the species which we are considering, that all incipient zoosporangial thalli are potential male and female cells which, under certain conditions, become somewhat differentiated and function in the formation of resting spores. The use of the terms "antheridium" and "oogonium" to denote the smaller and larger fusion thalli, respectively, is unfortunate and misleading. These terms, in their proper sense, refer to gametangia producing male and female gametes. Consequently, these thalli, when they fuse, may more properly be referred to as male and female thalli.

All our observations indicate that this species is haplosynoecious and that sex is phenotypically determined. Upon the basis of such a hypothesis the wide range of variation in sexual expression and the ability of certain environmental factors to influence such variation can, to some extent, be explained. Conclusive evidence of the truth of the hypothesis, however, must await the results of much more experimentation and cytological demonstration of meiosis occurring in the germination of the resting spores.

DISCUSSION

The foregoing observations on resting spore formation in the species with which we are dealing show conclusively that distinctions drawn between sexual and asexual species are totally unwarranted. The formation of resting spores of the *Olpidiopsis* type does not involve fusions between genotypically differentiated gametes but apparently merely represents a reaction between incipient zoosporangia which, under certain conditions, may become somewhat modified to function in resting spore formation. It has been demonstrated, moreover, that such fusions are in no way essential to resting spore development and that, in this particular species, the percentage of sexual spores formed may vary over a wide range in accordance with the temperature and other obscure external factors. Consequently, it is obvious that *Pseudolpidium* should be merged with *Olpidiopsis* and that the description of the latter genus should be amended to include species with smooth and

spiny zoosporangia which may form either sexual or asexual resting spores. The author is accordingly revising the generic diagnosis as follows:

OLPIDIOPSIS Cornu, Ann. Sci. Nat. V, **15**: 114. 1872. *Pleocystidium* Fisch, Sitz.-ber. Phys. Med. Soc. Erlangen **16**: 29–66. 1884. *Diplophysa* Schroeter in Cohn's Kryptog. Fl. Schlesiens **3**: 175–197. 1889. *Olpidiopsis* (Cornu) Fischer, Rabenhorst Kryptog. Fl. **1**[4]: 37. 1892. *Pseudolpidium* Fischer in Rabenhorst Kryptog. Fl. **1**[4]: 33. 1892. *Pseudolpidiopsis* Minden. Krypt. Fl. Mark Brandenburg **5**: 209–422. 1911.

Thallo intramatricali, monocentrico, holcarpico, primum nudiusculo (ut videtur) sed protoplasma hospitis inmixto, maturitate distincto pariete cellulosam habente disiuncto. Zoosporangiis solitariis vel numerosis, hyalinis vel parce granulosis, levibus vel echinulatis, globosis, ovalibus-ellipsoideis, cylindriceis, sacculatis vel irregularibus, cum una aut amplius tubulis exeuntibus, latis, acutis vel cylindriceis, rectis, curvis spiriformibus, brevibus vel elongatis, quae usque ad parietem matricis pertinere aut etiam se extra proicere solent. Zoosporis hyalinis, minutissime granulatis, interdum cum gutta contrahende, ovali, ellipsoideo, vel aliqua ex parte elongata atque reniformi; hetero- et isoconti flagellis a latere prope anteriorem partem insertis, flagello breviore protinus, longiore retro plerumque derecto; maturis emergentibus subitoque enatantibus vel interdum quiete cumulo ostio tubulae aliquamdiu manentibus; aequaliter haud emicatim movent ex occasione flagellatis retractis tranquilliter quiescentes. Sporis perdurantibus, gamicis, agamicis vel parthenogeneticis, ovalibus ellipsoideisve, hyalinis, brunneis, levibus, verruciformibus, undulatis, echinulatis, unum aut amplius globulos refringentes magnos parvosve aut habentibus aut carentibus; antheridia, cum adsunt, solitaria vel numerosa, hyalina, levia, spiniformia vel echinulata. Germinatio directa, tubula exeunte formata et biflagellatis zoosporis liberatis.

Thallus intramatrical, monocentric, holocarpic, appearing more or less naked but immiscible with the host protoplasm when young, becoming invested with a definite cellulose wall at maturity. Zoosporangia solitary or numerous, hyaline or slightly granular, smooth or spiny, spherical, oval, ellipsoidal, elongate, sac-like or irregular with one or several broad, tapering or cylindrical, straight, curved, coiled, short or elongate exit tubes which may end flush with the surface of the host cell or may project beyond it. Zoospores hyaline with numerous minute granules, and occasionally a contractile vacuole, oval, ellipsoidal, or somewhat elongate and reniform, hetero- and isocont; flagella inserted laterally near the anterior end, the shorter one usually directed forward and the longer backward; emerging fully formed and swimming directly away or occasionally lying quiescent in a mass for a moment at the mouth of the exit tube; movement even, not darting, interrupted by one or several rest periods during which the flagella may be retracted. Resting spores sexual and asexual or parthenogenetic, oval or ellipsoidal, hyaline, brown, smooth, warty, undulating or wavy, spiny, with or without one or several large or small refringent globules; male cells, when present, single or numerous, hyaline, spherical, smooth, warty or spiny. Germination of the resting spore direct by formation of an exit tube and liberation of biflagellate zoospores.

Few of the species of *Pseudolpidium* and *Olpidiopsis* which have been described have been adequately studied and we have very little accurate knowledge of their variability and host relationships. Yet it is primarily upon the basis of the host range and exospore variations that these species have been determined. It has been pointed out above that the resting spores of several species which are now considered as distinct are simulated in monospore cultures of the extremely variable species which we are considering. In view of this, it does not appear that the character of the exospore is a suitable, fundamental diagnostic character. It seems highly probable that many of the species which have been described may prove to be synonymous with or nothing more than physiological strains of a few legitimate species. This new species, likewise, may be synonymous with several others which are at present considered distinct but, until all these related species have been critically studied in monospore cultures, the exact identity and relationships of this species must remain in doubt. For this reason I am provisionally naming the species until the genus as a whole is better known.

Olpidiopsis Achlyae McLarty sp. nov. (ad int.). Zoosporangiis solitariis vel numerosis, plerumque in matricis cellibus turgidis terminalibus vel intercalaribus positis; brunneolis, parce granulatis, maturitate pariete cellulosam habente circumvallatis, levibus vel spinis angustis vel crassis quae cellulosa carent; sphaericis, ovalibus, ellipsoideis vel elongatis, magnitudine variis, 13.2–112.4 μ diametro × 115.0–666.4 μ; tubulis exeuntibus (1–3 numero) quae saepissime extra superficiem hospitis longe pertinent. Zoosporis hyalinis minutissime granulatis, ovalibus, sphaericis, vel parce reniformibus, 3.2–5.7 μ × 2.9–4.3 μ, plerumque c. 3.1 × 4.2 μ, cum duobus subaequalibus flagellis a latere prope anteriorem partem coniunctis. Sporis perdurantibus gamicis, agamicis, vel parthenogeneticis, sphaericis vel ovalibus, 22.8–122.4 μ (plerumque c. 50.0 × 41.0 μ), brunneis, cum uno (compluribus rarius) permagno globulo refringente. Endosporio cellulosam habente, levi, 1.0–1.5 μ diametro. Episporio cellulosa carente, 1.0–11.4 μ, spinis verruciformibus, parvis vel magnis, basi angusto vel lato, fibrillis capilliformibus vel cum margine levi, undulato vel paullum serrato. Antheridia, cum adsunt, contenta in oogonium interdum (non tamen semper) ejiciunt forma zoosporangiis similia, 1–3 uni oogonio adiunctis, sphaericis, vel ovalibus, tenui pariete, levibus, interdum in episporio conclusa. Spora perdurans germinatione in sporangium transformatur, zoosporis tubula exeunte liberatis.

Zoosporangia solitary or numerous, usually localized in a terminal or intercalary swelling of the host filament, slightly brown and granular, enclosed at maturity by a cellulose wall, smooth or covered with fine or coarse non-cellulose bristles; spherical, oval, ellipsoidal or elongate, variable in size, 13.2–112.4 μ diam. × 115.0–666.4 μ; one to three exit tubes which may extend considerably beyond the surface of the host filament. Zoospores hyaline with numerous small granules, oval, spherical, or somewhat reniform, 2.3–5.7 μ × 2.9–4.3 μ, usually about 4.2 × 3.1 μ, with two approximately equal flagella attached laterally near the anterior end. Resting spores sexual and asexual or parthenogenetic, spherical or oval, 22.8–122.4 μ (usually about 50.0 × 41.0 μ), brown, with several or commonly one, large refringent globule.

Endospore composed of cellulose, smooth, 1.0–1.5 μ in thickness. Exospore not composed of cellulose, varying from 1.0–11.4 μ in thickness, with warty protuberances, small or large, narrow or broad-based spines, hair-like fibrillae or with an entire, undulant or slightly serrate margin. Male cells, when present, may or may not discharge contents into female thallus, similar in appearance to zoosporangia, one to three attached to one female thallus, spherical or oval, thin-walled, smooth, sometimes embedded in the exospore. Resting spore in germination transformed into a sporangium liberating zoospores by means of an exit tube.

Parasitic in *Achlya flagellata* Coker from a pool on the campus of the University of Western Ontario, London, Canada, September 1937.

It has been shown by the author (1939) that the spiny bodies which Fischer described as resting spores of *Pseudolpidium Saprolegniae* and *P. fusiforme* are merely rough walled zoosporangia and that, inasmuch as they all occur in monospore cultures of *O. Achlyae*, the sporangial types which Fischer regarded as diagnostic of his two species cannot be regarded as being limited to any one organism. This viewpoint has been confirmed by the subsequent observations of Shanor (1939). Consequently, *P. Saprolegniae* must be recombined with *O. Saprolegniae* while *P. fusiforme* and *O. minor* must be recombined under the original name, *O. fusiformis*, as Shanor has already suggested. *Pseudolpidium stellatum* was described by Sawada in 1912 (Tokunaga 1933) when he observed resting spores, similar to those of *O. minor* but without adjacent cells, occurring frequently in association with *P. fusiforme*. In view of our observations on *O. Achlyae* it seems advisable to combine this species also with *O. fusiformis* and to consider the latter as a sexual-asexual species.

Olpidiopsis Aphanomycis was originally described by Cornu (1872) and included as a member of the genus although he did not observe resting spores. Consequently Fischer (1892) transferred this species to *Pseudolpidium* as *P. Aphanomycis*. Dangeard (1891) illustrated a resting spore of *O. Aphanomycis* with no adjacent cell. Butler considered this to be the true resting spore of *P. Aphanomycis*. Subsequently, Petersen (1910) described sexual resting spores for *O. Aphanomycis* and commented on the similarity between this species and *O. Saprolegniae*. Barrett (1912) described another species, *O. luxurians*, occurring in filaments of *Aphanomyces*. Shanor (1939) has discussed the similarities which exist between all of these parasites of *Aphanomyces* which have been reported by Cornu (1872), Dangeard (1891), Butler (1907), Petersen (1910), and Barrett (1912) and suggests that later investigations may prove that they are all synonymous with Cornu's original species. This may be true, but at the present time it seems advisable to maintain Barrett's species and to combine the remainder of the sexual and asexual parasites of *Aphanomyces* which have been described under Cornu's original name *O. Aphanomycis*.

Only one of the resting spores which Cornu (1872) illustrated for *O. incrassata* possessed an antheridial cell. Consequently Fischer (1892) tentatively transferred the species to *Pseudolpidium* as *P. incrassata*. Since that time Sparrow (1933) has reported *P. incrassata*, while Petersen (1910) considers this species as synonymous with *P. Saprolegniae*. Maurizio (1895) claims that the resting spores of *O. incrassata* are identical with those of *O. major*. It appears that Cornu (1872), Maurizio (1895), and Sparrow (1933) were dealing with the same organism. Accordingly the author proposes to combine *P. incrassata* and *O. major*, which has not been observed since its description, under Cornu's original name, *O. incrassata*, and to consider the species as one which produces sexual and asexual resting spores.

Pseudolpidium Pythii and *P. gracile*, as described by Butler (1907), possess relatively thin-walled resting spores covered with fine spines. Very little is known of these species, although each has been observed since Butler's time. The resting spores of these species, as they are illustrated in the literature, appear very similar in appearance to spiny zoosporangia. Until they are re-collected and critically examined, these species may be transferred to *Olpidiopsis* as strictly asexual species.

Pseudolpidium glenodinianum and *P. Sphaeritae* (Fischer 1892) and *P. deformans* (Serbinow 1907), of which no resting spores are known, may be transferred to the genus *Olpidiopsis* on the basis of their biflagellate zoospores and maintained as very doubtful species until their real identity can be demonstrated.

SUMMARY

A new species, *Olpidiopsis Achlyae*, which produces smooth and spiny-walled zoosporangia and sexual and asexual resting spores, has been described. The genus *Pseudolpidium* has been merged with *Olpidiopsis* and the diagnosis of the latter has been revised accordingly.

Variations in the size and shape of the zoosporangia seem to depend directly upon the amount of nourishment available to the developing thalli. Non-cellulose bristles appear to be formed by a localized deposition of host protoplasm upon the surface of the incipient zoosporangium.

Evidence has been presented in support of the view that the exospore, which, in contrast to the endospore, is not composed of cellulose, is formed by a localized deposition of host protoplasm upon the surface of the parasite.

Resting spores, which have been described as characteristic of several species of *Olpidiopsis*, are commonly simulated in pure cultures of *O. Achlyae*. The marked variability of the exospore in this species indicates that it is not a suitable diagnostic character upon which to base specific distinctions.

Fusions between thalli are in no way essential to the formation of rest-

ing spores by this species. *O. Achlyae* is, apparently, haplosynoecious, and sex, when present, is phenotypically determined.

This study of pure cultures of *O. Achlyae* clearly indicates the need for a critical re-examination of all species of *Olpidiopsis*, which, for the most part, have been very inadequately studied.

The writer wishes to express his appreciation and thanks to Prof. John S. Karling, under whose direction this investigation has been carried on, for his generous assistance and stimulating criticism; to Prof. Helen Berdan, who provided the original cultures from which this species was isolated; and to Prof. J. N. Couch for the identification of the species of *Achlya*. Courtesies extended by the writer's colleagues on the Botany faculty of Dartmouth College have greatly facilitated the completion of this study.

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NEW OR NOTEWORTHY SOUTH AMERICAN ERIOCAULACEAE

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Recent collections of South American plants sent to the writer for determination have brought to light a number of hitherto undescribed species and varieties in the *Eriocaulaceae* and have revealed the desirability of reducing a specific combination to varietal rank.

Paepalanthus Archeri Moldenke, sp. nov. Herba acaulis nana; foliis caespitosis recurvatis linearibus, ad basim densissime longeque villosis, ad apicem utrinque glabratis; pedunculis stramineis 3-costatis densiuscule longeque pubescentibus; vaginis subglabratis, ad apicem oblique lobatis.

Dwarf stemless herb; leaves tufted, recurved, appressed to the ground, olivaceous, linear, 4–10 mm. long, 0.5–1 mm. wide at the middle, blunt at apex, not fenestrate, very densely long-villous with silky-white hairs at the base, glabrous on both surfaces at apex, the basal villosity forming a very dense and conspicuous white cottony tuft or cushion at the base of the plant; peduncles stramineous, very slender, 3–4.5 cm. long, twisted, 3-costate, rather densely long-pubescent with divergent whitish gland-tipped hairs; sheaths closely appressed to the peduncles, about 1 cm. long, twisted, many-costate, subglabrate except for the long-ciliate obliquely lobed mouth, the lobe 2–3 mm. long, acuminate and somewhat recurved at apex; heads hemispheric, about 3 mm. high and 6 mm. in diameter, densely many-flowered; involucral bractlets numerous, many-seriate, chestnut-brown (the inner ones lighter), obovate or spatulate, 1.9–2.5 mm. long, 0.9–1.4 mm. wide, rounded at apex, glabrous on both surfaces; receptacle very densely long-villous with white hair; receptacular bractlets hyaline, obovate, about 3 mm. long and 1.2 mm. wide, rounded at apex, long-cuneate at base, appressed-pilose on the back; staminate florets: long-pedicellate; sepals 3, connate at the base only, hyaline, obovate-elliptic, about 1.9 mm. long and 0.7 mm. wide, rounded at apex, densely appressed-villous on the back toward the apex; petals connate into a hyaline, hollow, glabrous, minutely 3-lobed, eglandular tube; stamens 3, less than 1 mm. long, white; pistillate florets: short-pedicellate or subsessile; sepals 3, connate at base, hyaline, about 1.2 mm. long and 0.3 mm. wide, obovate, rounded at apex, densely pilose on the back toward the apex; petals 3, separate, minute, orbicular, about 0.3 mm. long and wide, glabrous, eglandular; pistil about 0.7 mm. long; styles, stigmas, and style-appendages 3 each, white.

BRAZIL—MINAS GERAES: Serra do Cipó, alt. 1800 m., *William Andrew Archer 3677*, August 5, 1936, TYPE; in the United States National Herbarium at Washington.

Paepalanthus Killipii Moldenke, sp. nov. Herba perennis; caule elongato folioso stolonifero; foliis imbricatis graminoidiis subacutis integris utrinque sparse obscureque puberulentibus et plusminus albido-pilosis, glabrescentibus nitidis; vaginis adpressis sparse piloso-hirsutulis, ad apicem oblique lobatis; pedunculis tenuibus numerosis erectis stramineis 2-costatis glabris nitidis; capitulis cinereis.

Perennial herb; stem slender, elongate, to 17 or more cm. long, decumbent at base, erect at apex, leafy; abbreviated branches issuing from the stem near its base in stolon-like fashion, bearing diminutive young "plants" with very narrow leaves, 2 or 3 abbreviated peduncles, and tiny few-flowered heads; leaves (on normal plants) overlapping, grass-like, olivaceous, 3.5–7 cm. long, 1.5–7 mm. wide (usually 5–7 mm. wide), subacute at apex, entire, sparsely and obscurely puberulent on both surfaces, with scattered long and whitish pilose hairs interspersed, especially toward the base, glabrescent in age, shiny on both surfaces, not fenestrate, many-nerved; sheaths tubular, closely appressed to the peduncles, 3–5 cm. long (smaller on the basal stolons), sparsely pilose with long, scattered, weak, whitish, hirsutulous, spreading hairs, more densely so at the obliquely lobed mouth, the lobe 2.5–4 mm. long, attenuate at apex; peduncles slender, numerous, about 50 per plant (except on the basal stolons), erect, 9–27 cm. long, stramineous, 2-costate, glabrous and shiny throughout; heads hemispheric, ashy-gray, 3–6 mm. in diameter (much smaller on basal stolons); involucral and receptacular bractlets similar, oblong or obovate, dark-brown or blackish, about 1.2 mm. long and 0.7 mm. wide, rounded at apex, glabrous on both surfaces except for a tuft of short erect hairs at the apex; receptacle densely long-villous; staminate florets: short-pedicellate; sepals 3, very slightly connate only at the very base, dark-brown, obovate, about 1 mm. long and 0.7 mm. wide, rounded at apex, glabrous on both surfaces; petals connate into a hyaline, hollow, glabrous, eglandular, minutely 3-lobed tube; stamens 3, about 1.4 mm. long, white, glabrous; pistillate florets: very short-pedicellate; sepals 3, connate only at the very base, obovate, dark-brown toward apex, about 1.4 mm. long and 0.6 mm. wide, rounded at apex, appressed-villous on the back; petals 3, free, hyaline, narrowly oblanceolate, about 1.4 mm. long and 0.4 mm. wide, rounded at apex, densely long-villous; pistil about 1.4 mm. long, glabrous; styles, stigmas, and style-appendages 3 each, glabrous.

COLOMBIA—SANTANDER SUR: Eastern Cordillera, Mesa de los Santos, marshy land, alt. 1500 m., *Ellsworth Paine Killip & Albert Charles Smith 15,299*, between December 11 and 15, 1926, TYPE; in the United States National Herbarium at Washington. Named in honor of E. P. Killip.

Paepalanthus lodiculoides Moldenke, sp. nov. Herba perennis; caulis abbreviatis lignosis caespitosis densissime albo-villosis vel -tomentosis; foliis linearibus densissime imbricatis valde adpressis glabris; pedunculis gracillimis abbreviatis sparsissime pilosulis vel glabris; capitulis solitariis.

Perennial herb, very densely tufted; stems apparently much abbreviated and woody at base, 1 or 2 cm. long, very densely white-villous or -tomentose with long cottony hair which completely hides the stem and almost hides the leaves; leaves very numerous, linear, about 2 mm. long, closely appressed to the stem and very densely imbricate, glabrous, blunt at apex; no venation obvious on either surface; peduncles solitary, terminating the stem, very slender or subfiliform, 5–6 mm. long, very sparsely white-pilosulous or glabrous and shiny; heads solitary, hemispheric, about 2 mm. in diameter, few-flowered; involucral bractlets 2 or 3, ovate, about 2 mm. long and wide, acute at apex, brunneous, glabrous, shiny; staminate florets: sepals 3, firm and rigid, dark-brown or blackish, elliptic, about 2 mm. long and 0.7 mm. wide, acute or short-acuminate at apex and bearing a dense tuft of villous erect hairs on the back at the apex; petals united into a membranous 3-lobed

tube about 1.5 mm. long, the lobes sharply acuminate or apiculate, glabrous; stamens 3, exserted; pistillate florets: sepals 3, practically separate to the base, elliptic, dark-brown or blackish, firm and rigid, navicular, about 2.2 mm. long and 1 mm. wide, sharply acute at apex, very densely villous with an erect tuft of whitish hairs at the apex on the back; petals 3, separate, elliptic, navicular, about 2.2 mm. long and 0.8 mm. wide, firm, somewhat stramineous, subtranslucent, subacute, eglandular, densely white-villous with erect white hairs from the middle to the apex; ovary conspicuously 3-lobed, about 1 mm. long and wide, glabrous, plainly 3-celled; style-branches 3, linear, about 1.2 mm. long, white, papillose at apex; stigmas 3, linear, about 1.4 mm. long, simple, unbranched.

COLOMBIA—BOYACÁ: Cordillera oriental, Nevadodel Cocuy, high valley of Las Lagunillas, alt. 4000–4300 m., *José Cuatrecasas 1537*, September 12, 1938, TYPE; in the United States National Herbarium at Washington.

Paepalanthus paramensis Moldenke, sp. nov. Herba acaulis; foliis caespitosis graminoideis valde villoso-pilosis; vaginis late cylindricis subglabris vel sparsissime pilosis, ad apicem subtruncatis undulatis; pedunculis mediocriter tenuibus, versus apicem dense villoso-pubescentibus, versus basim glabrescentibus; capitulis compositis griseis.

Stemless herb; leaves tufted, olivaceous, grass-like, 2.5–6 cm. long, 2–6 mm. wide, broadest at the base, sharply subulate-tipped at apex, entire, abundantly villous-pilose with long, whitish, shaggy, spreading hair on both surfaces, many-nerved, not fenestrate; sheaths rather broadly cylindric, about 2.5 cm. long, subglabrous or very sparsely pilose with widely scattered hairs, especially at the apex; mouth subtruncate, almost regular, the margins slightly flaring and undulate-lobed; peduncles medium-slender, 4–8 per plant, 5–7 cm. long, densely villous-pubescent with incanous spreading hairs toward the apex, much more sparsely so or glabrescent at base; heads hemispheric or almost spherical, 1–1.4 cm. in diameter, ashy-gray, compound, composed of about 6 smaller sessile heads; involucral bractlets brunneous, broadly oblong or ovate, about 3.5 mm. long and 3.4 mm. wide, usually 2-lobed at the broadly rounded apex, truncate at base, lightly villosulous-pilose toward the apex outside; receptacular bractlets oblong, about 2.9 mm. long and 1.4 mm. wide, subacute at apex, densely villous on the back toward the apex, with a dense tuft of erect hair at the very apex; staminate florets: short-pedicellate; sepals 3, brown, connate at the very base, obovate, about 2.4 mm. long and 0.9 mm. wide, rounded or subacute at apex, cuneate at base, densely white-villous at the apex on the back with an erect conspicuous tuft of hair; free portion of petals narrow-elliptic, hyaline, about 1.2 mm. long and 0.5 mm. wide, acute at both ends, eglandular, connate at base only, glabrous; stamens 3, about 1.4 mm. long, the filaments white, anthers yellowish; pistillate florets: short-pedicellate; sepals 3, brown, obovate, about 1.9 mm. long and 0.9 mm. wide, subacute at apex, densely villous on the back with a conspicuous tuft of white erect hair at the apex; petals 3, hyaline, free, elliptic, about 0.9 mm. long and 0.4 mm. wide, very densely tufted-villous on the back; pistil about 1.2 mm. long; styles, stigmas, and style-appendages 3 each; ovary minutely puberulent.

COLOMBIA—NORTE DE SANTANDER: Páramo del Hatico, en route from Toledo to Pamplona, alt. about 2900 m., *E. P. Killip & A. C. Smith 20,622*, March 12 or 13, 1927, TYPE; in the United States National Herbarium at Washington.

Paepalanthus viscosus Moldenke, sp. nov. Herba perennis; caule tenui dense folioso bifurcato; foliis linearibus viscidis villosis glabrescentibus; vaginis adpressis albido-villosis glabrescentibus, ad apicem oblique lobatis; pedunculis filiformibus stramineis 2-costatis densiuscule piloso-pubescentibus; capitulis griseis.

Perennial herb; stems slender, 1–3 cm. long, apparently creeping, rooting at the nodes, very leafy, bifurcate; leaves olivaceous, linear, viscid, 5–10 mm. long, 0.5 mm. wide or less, blunt at apex, shaggy-villous when young and toward the base, glabrescent in age, closely imbricate and appressed to the stems when young, more divaricate in age, 1-nerved, often canaliculate, not fenestrate; sheaths narrow, closely appressed to the peduncles, 6–12 mm. long, white-villous with long divergent hair, glabrescent in age, its mouth very obliquely lobed, the lobe narrow-lanceolate, about 2 mm. long, slightly divergent, acuminate; peduncles very slender or filiform, stramineous during anthesis, later brunnescent, 2-costate, hardly twisted, 4–7 cm. long, rather densely pilose-pubescent; heads gray, hemispheric, 2–4 mm. wide; involucral bractlets stramineous, ovate, about 0.7 mm. long and 0.4 mm. wide, acute at apex, glabrous; receptacle densely long-villous; receptacular bractlets oblong, about 1.4 mm. long and 0.5 mm. wide, obtuse at apex, stramineous in the center, hyaline at the margins, tufted-villous at the apex on the back; staminate florets: short-pedicellate; sepals 3, connate at the very base only, obovate, about 1 mm. long and 0.5 mm. wide, rounded at apex, cuneate at base, tufted-villous at the apex on the back; petals 3, connate into a hyaline, hollow, eglandular, glabrous, minutely 3-lobed tube; stamens 3, about 1 mm. long, white; pistillate florets: short-pedicellate; sepals 3, connate at the base only, stramineous, obovate, about 0.9 mm. long and 0.4 mm. wide, glabrous except for 2 or 3 erect villous hairs at the apex (or densely tufted) on the back; petals 3, free, hyaline, narrow-elliptic, about 1.2 mm. long and 0.3 mm. wide, acute at apex, tufted-villous on the back at the apex; pistil about 1.2 mm. long; styles, stigmas, and style-appendages 3 each; ovary glabrous.

SURINAM: Sandrij I, *William Andrew Archer 2836* between November 14 and 25, 1934, TYPE; in the United States National Herbarium at Washington. The collector describes the leaves as sticky.

SYNGONANTHUS CAULESCENS (Poir.) Ruhl. var. **angustifolius** Moldenke, var. nov. Haec varietas a forma typica speciei recedit foliis longioris angustioris 2–3.5 cm. longis, 0.5–2 mm. latis, ad apicem attenuatis argute acutis.

This variety differs from the typical form of the species in its uniformly longer and narrower leaves, which are 2–3.5 cm. long and 0.5–2 mm. wide, gradually attenuate to the sharply acute apex.

COLOMBIA: Los Llanos, Méta, in a bog about 20 km. south and 30° west of Orocué, alt. about 150 m., *Oscar Haught 2747*, April 9, 1939, TYPE; in the Britton Herbarium at the New York Botanical Garden. It is said to be a common herb in bogs of the Llanos region. The typical form of the species is well represented by *Haught 2355* from Magdalena.

SYNGONANTHUS CAULESCENS (Poir.) Ruhl. var. **procerus** (Klotzsch) Moldenke, comb. nov. *Paepalanthus procerus* Klotzsch in Schomb., Reise in Brit. Guian. **3**: 1115. 1848.

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